FITNESS CONSEQUENCES OF AVIAN HABITAT SELECTION IN DYNAMIC LANDSCAPES: MULTI-SCALE EVALUATIONS IN NORTHERN PINTAILS

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ABSTRACT

According to theory, habitat selection by organisms should reflect the associated probability of survival or reproductive success. Understanding habitat selection, at multiple scales, is of interest not only from a theoretical perspective, but from an applied perspective for species conservation. Northern pintails (*Anas acuta*) are migratory, temperate-nesting birds that breed in greatest concentrations in the prairies of North America. Declining populations suggest that habitat loss and changing land use may have decoupled formerly reliable fitness cues from selection of suitable nest habitat.

I used data from 62 waterfowl nesting study sites in prairie Canada (1997–2009), to examine whether nest survival, a primary fitness metric, at nest and habitat patch scales, was predictive of habitat selection at corresponding scales. In addition, I used systematic long-term annual pintail population monitoring data (1961–2009), and recruitment indices (juvenile:adult female ratio) from hunter harvest, to examine adaptive habitat selection among landscapes within the Prairie Pothole Region (PPR). The influences of breeding population density and landscape composition were examined at all scales.

At nest and patch scales, pintail nest survival varied with nest initiation date, nest habitat, pair density, and landscape composition. Nest habitat preference reflected patterns in nest survival suggesting nest habitat preference is adaptive. Preference was generally low for habitats with low nest survival (e.g., spring-seeded cropland) and high for habitats with high nest survival (e.g., idle grassland). Differences in preference among habitats weakened at high breeding density and in landscapes with more grassland.

Population-level recruitment tended to be greater when pintails settled in landscapes that were wetter than normal, contained more grassland, and were moderately variable in local

elevation. Pintails were strongly associated with wetter than normal landscapes but shifted into cropland-dominated landscapes and flatter landscapes when populations were high. My results indicated that pintails express adaptive habitat associations with density-dependence acting through buffer mechanisms.

Finally, I use the results of the above analyses to, 1) model and map the estimated long-term average spatial abundance of pintail pairs across the PPR as a function of landscape-level covariates, and 2) construct a deterministic model predicting pintail productivity given habitat and landscape attributes. These models allow conservation efforts to be targeted to affect the most birds, and they allow estimation of the demographic response to conservation actions.

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Deserving of special mention are the many biologists, pilots, and ground crews in the U. S. Fish and Wildlife Service and Canadian Wildlife Service who over the years have collected and maintained the annual May Waterfowl Breeding Population and Habitat Survey data. This dataset is one of the longest running and most extensive wildlife surveys in the world and the data provided is invaluable in helping to understanding the population dynamics and habitat associations of North American waterfowl.

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"We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect."

-Aldo Leopold,

Foreword to A Sand County Almanac (1949)

DEDICATION

I dedicate this dissertation to my parents, Thomas and Lorraine Devries. Their love, support, and advice throughout my life has allowed me to pursue my interests in the natural world. For that I am eternally grateful.

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CHAPTER 1. INTRODUCTION

1.1 General Introduction and Theoretical Framework

The field of population ecology is predicated on empirical evidence that the intrinsic ability of populations to grow is ultimately limited by the environment. Indeed, density-dependence has been demonstrated either proximately through social interactions or ultimately through resource limitation (Turchin 2001). The life cycle requirements of most species are fulfilled in environments where resources vary in quantity and quality across space and time. Given gradients in the quality of resources among habitats, individuals should select habitats that maximize their fitness or minimize the cost-benefit ratio of occupying specific habitats (Fretwell and Lucas 1969, Southwood 1977, Jaenike and Holt 1991, Martin 1998, Misenhelter and Rotenberry 2000). Ultimately, responses to an environment that improve survival or reproduction (fitness) should persist (Rosenzweig 1974).

Habitat selection is generally assumed to be a hierarchical process reflecting decisions made at a multitude of scales (Johnson 1980, Chalfoun and Martin 2007). Fitness may depend on characteristics of a specific location, patch, landscape or geographic region (e.g., Orians and Wittenberger 1991, Battin and Lawler 2006, Howerter et al. 2008). Because *a priori* knowledge of actual fitness is generally unavailable, we expect successful species to have evolved the ability to identify proximate cues that reliably reflect fitness potential at the scales that are important (Misenhelter and Rotenberry 2000, Rolstad et al. 2000). Hence, in the absence of disrupting cues (e.g., Schlaepfer et al. 2002, Gilroy and Sutherland 2007), patterns of habitat use by individuals should emerge as a consequence of behaviours adapted to maximize fitness (Clark and Shutler 1999, Jones 2001, Kristan et al. 2007). Specifically, preferential use is expected at

sites, or among patches, landscapes (composites of patches and matrix), and regions (composites of landscapes) where expected fitness is high.

However, it is expected that habitats may be limited in the number of individuals they can support and density-dependent mechanisms will eventually begin to reduce fitness (e.g., Fretwell and Lucas 1969, Brown 1969). Alternate mechanisms for density-dependent habitat selection have been proposed. Most attention has focused on the Fretwell and Lucas (1969) 'ideal-free' and 'ideal-dominance' distributions. Under an 'ideal-free' distribution, individuals are 'free' (or unlimited) in their ability to choose among habitats and will initially select the habitat that confers the highest fitness; but fitness declines as density within the habitat increases to a point that fitness is equal to that in an alternate habitat. Thus, density within and among habitats is adjusted so that all individuals experience similar fitness regardless of habitat choice. Under an 'ideal-dominance' distribution, individuals are limited by competitive ability and highest quality habitat is monopolized by dominant individuals forcing subordinates into lower fitness habitat thereby maintaining a fitness differential among habitats. When Fretwell and Lucas'(1969) ground-breaking ideas were being advanced, Brown (1969) proposed a "buffer effect" model, similar to the ideal-dominance distribution, whereby fitness varies among habitats, density within habitats is limited, and individuals are forced into lower quality habitats at high population levels, reducing per capita fitness (e.g., Potts et al. 1980, Pulliam et al. 1992). In the latter case, density dependence is observed not at the patch scale but at the landscape scale (Pulliam 1996). Under the Brown model, it follows that a greater proportion of nest sites or individuals within a population will occur in relatively low fitness patches or landscapes when populations are high (i.e., selection pattern changes with population density; see also Rodenhouse et al. 1997). While intraspecific density is most often examined in studies of

density-dependence, interspecific interactions can affect fitness processes as well (Cody 1981, Elmberg et al. 2003), for instance, when closely related species compete for both space and resources (Nudds 1983, Robinson and Terborgh 1995, Nummi and Väänänen 2001, Gurd 2008).

Individual responses to fitness cues and realized fitness translate into the habitat-mediated demographic processes that regulate natural populations (Pulliam 1996). Where fragmentation isolates suitable habitat, habitat selection may result in a metapopulation structure and source-sink dynamics (Pulliam 1988, Pulliam 1996, Opdam and Wiens 2002). An important assumption of adaptive habitat selection in conjunction with population regulation is that individuals can accurately assess habitat quality and settle in better habitat as opportunities arise. When habitat is altered rapidly or in novel ways (e.g., often due to human alteration) that decouple fitness from cues used by individuals, preferred habitat may become a population sink leading to an ecological 'trap' (Gates and Gysel 1978, Best 1986, Schlaepfer et al. 2002, Arlt and Part 2007). Ecological traps are more detrimental to population trajectory than sink habitats because traps are preferentially selected (Kristan 2003) whereas sink habitat may often serve as a "holding area" for individuals until better habitat becomes available. Recently, the avoidance of high quality habitat due to erroneous perceived cues has been recognized as an alternative process that could disrupt an animal's ability to relate habitat fitness and use (i.e., perceptual traps; Gilroy and Sutherland 2007, Patten and Kelly 2010). Because habitats also may be occupied regardless of inherent fitness (Van Horne 1983, Battin 2004), inferring habitat preference requires information not only on use, but also on use relative to potential habitat cues and links between habitat cues and fitness components at appropriate scales (Clark and Shutler 1999, Arlt and Part 2007, Chalfoun and Martin 2007).

While questions and advances in population ecology and evolutionary biology are of considerable theoretical interest, their ramifications have very tangible applications when population and conservation management strategies depend on this knowledge (Colyvan 2008). The importance of understanding the demographic consequences of species' interactions with their environment is paramount in the various disciplines of biodiversity conservation. Most often, conservation activities focus on habitats and their role in providing resources and demographic benefits (survival, reproductive success) for associated species. Improving our understanding of these complex relationships, and the spatial and temporal context in which they occur, provides direction for conservation action (e.g., Schumaker et al. 2014).

Prairie nesting waterfowl are well suited to evaluating predictions arising from habitat selection theory and linking relevant findings to habitat conservation and population management. At the breeding range scale in North America, extensive annual duck and pond survey data reveal much variation in duck settling patterns among biomes and landscapes that can be linked to regional environmental and habitat conditions (e.g., ponds). Field studies can provide large samples of nests from which nest survival and habitat use patterns may be linked. Further, prairie and wetland habitats have undergone extensive modification due to agricultural land use and hence it is likely that variation in components of fitness is associated with habitat loss and fragmentation.

Habitat fragmentation and loss are often cited as the primary threats to wildlife conservation from local to global scales (Noss 1991, Wilcove et al. 1986, Baillie et al. 2004). While habitat fragmentation and loss occur through natural processes, the most prevalent cause is the expansion and intensification of human land use, primarily agriculture (Andrèn 1994, 1996). Opdam and Wiens (2002) argue that fragmentation *per se* is only one of a larger set of

anthropogenic disturbances including dissection, perforation, shrinkage, and ultimately loss through attrition, that result from patterns of human land use. Associated effects include decreasing patch size, increasing edge, decreasing patch continuity, increasing patch isolation, and an increasing background matrix (e.g., cropland). Habitat existing within the context of a fragmented landscape mosaic is subject to altered ecological processes that define costs and benefits for resident species (Opdam and Wiens 2002). Habitat loss, fragmentation, and changing land use practices have the potential to alter formerly reliable fitness cues to habitat choices with the potential for population level consequences.

1.2 Population ecology and conservation of northern pintails (*Anas acuta*)

Northern pintails (hereafter, pintails) are a migratory duck species that breed in greatest concentration in the Prairie Pothole Region (PPR) and Alaska, and winter in the southern USA and northern Mexico. Based on population size and density, the PPR is considered the primary breeding range (Bellrose 1980). Pintails are unique among North American dabbling ducks in their nomadic wanderings in response to annual wetland conditions and their propensity to select sparse nesting cover including cropland (Johnson and Grier 1988, Austin and Miller 1995). Declines since the 1970s, and current low populations, have sparked considerable concern regarding the potential for detrimental interactions between land use, habitat selection, and reproductive success in landscapes highly altered by agriculture (Miller and Duncan 1999, Podruzny et al. 2002, Hebert and Wassenaar 2005). Over the past century, the PPR has become one of the most intensively cropped landscapes in the world with over 80% of some municipalities/counties in cropland production (Foley et al. 2005, Statistics Canada 2011).

Several studies have suggested that historic landscape change in prairie Canada may have decreased waterfowl nest survival probability (Clark and Nudds 1991, Beauchamp et al. 1996,

Drever et al. 2004). Nest survival is a frequently measured demographic rate with important ramifications for reproductive success and hence, population growth in birds (Ricklefs 1969, Hoekman et al. 2002, Nagy and Holmes 2004, Mattsson and Cooper 2007). Further, nest survival varies at regional (Reynolds et al. 2001, Drever et al. 2007), landscape (Stephens et al. 2005), patch (Klett et al. 1988, Howerter 2003), and nest scales (Gloutney and Clark 1997, Guyn 2001, Howerter 2003). Under adaptive habitat selection, nest survival should be an important driver of habitat selection at these scales assuming of course that habitat cues reliably signal expected benefits.

The potential mechanisms for environment-mediated pintail population limitation and regulation are diverse and complex. Understanding relationships between pintail habitat selection and fitness will not only inform advances in habitat selection theory but also provide strong guidance for conservation. This is because processes that affect pintail habitat use and productivity relationships also may extend to other species that rely on similar habitat (e.g., Naugle et al. 2001, Skinner and Clark 2008).

1.3 Scale-specific habitat selection patterns and processes

In temperate breeding waterfowl, the annual process of migration to breeding areas presents a natural hierarchy of habitat choices in time and space as individuals decide where and when to breed. Johnson (1980) identified four levels of habitat selection: (1) geographic (or breeding) range; (2) home range; (3) habitat components within the home range; and, (4) specific resources (food items, nest sites). Based on natural selection theory, and evidence that pintails make active choices when settling and placing nest sites, I anticipate that, at all scales, patterns and strength of habitat selection should be positively related to metrics of fitness. In doing so, I assume that pintails are able to correctly assess relative quality and make the best choice(s) among available

habitats (Fretwell and Lucas 1969). Thus, I plan to test whether patterns in habitat selection at nest, patch, and landscape scales correspond to patterns of pintail reproductive success at corresponding scales. For this purpose, I define 1) nest sites by location-specific attributes of the nest itself, 2) patches as areas of typically uniform vegetation/land use composition (see Chapter 2, Table 2), and 3) landscapes as variably sized compositions of habitat patches and background matrix up to 41 km^2 in size under the assumption that pintails are able to assess broad characteristics of habitat at this scale.

At nest and patch scales, several processes related to nest predator behaviour likely create variation in nest survival, and thus nest habitat preference. For example, because nest predators may actively forage near wetland or other habitat edges (Paton 1993, Larivière and Messier 2000, Lahti 2001, Phillips et al. 2003), nesting females may avoid placing nests near wetlands and/or habitat edges. A trade-off may exist here as duckling survival may decrease with longer overland movements from the nest to wetlands (e.g., Talent et al. 1983, Bloom 2010, but see Guyn and Clark 1999). The size of the nest habitat patch may be a reliable cue given evidence that nest survival may be higher in large versus small habitat patches (e.g., Wilcove 1985, Sovada et al. 2000, Howerter 2003). However, these effects may be nonlinear and affected by other factors such as landscape composition (Clark and Nudds 1991, Clark et al. 1999, Horn et al. 2005). For example, the amount of grassland in the surrounding landscape has a well-established positive influence on waterfowl nest survival at landscape and nest scales (see below; Greenwood et al. 1995, Sovada et al. 2000, Reynolds et al. 2001). For ground-nesting waterfowl, nest survival typically varies among vegetation-land use categories (e.g., Greenwood et al. 1995, Cowardin et al. 1985, Klett et al. 1988) and is generally high in low disturbance habitat (e.g., idle grassland) and low in high disturbance habitat (e.g., spring-seeded croplands,

Klett et al. 1988, Greenwood et al. 1995, Emery et al. 2005), although these patterns may change through the nesting season (Emery et al. 2005). These habitat differences may reflect simple nest concealment potential (e.g., Livezey 1981, Dwernychuk and Boag 1972, Guyn 2001), but the importance of concealment may depend on the prevalence of avian predators in the local predator community (Clark and Nudds 1991).

Landscape-level selection cues are likely different but related to those used at nest and patch scales. Wetland and upland cues are likely readily assessed by breeding pintails and used in settling decisions (Krapu et al. 1997, Austin et al. 2001, Mack and Clark 2006). The number and size of wetlands are strong determinants of pintail and other duck species' occurrence (e.g., Cowardin et al. 1995, Bartzen 2008) which may affect density-dependent predation rates (e.g., Weller 1979). There may be trade-offs for pintails nesting in wetland-dense landscapes as predators actively cue in on wetland edges as profitable foraging sites (e.g., Larivière and Messier 2000, Phillips et al. 2003), potentially resulting in higher nest predation (e.g., Howerter 2003, Stephens et al. 2005). However, higher nest predation may be offset by higher duckling survival in wetland-rich landscapes (Rotella and Ratti 1992). Composition and fragmentation of upland habitat may affect settling decisions in several ways. The amount of grassland at a landscape scale likely affects the composition and foraging efficiency of prairie nest predator communities (Sargeant et al. 1993, Sovada et al. 2000, Phillips et al. 2003) such that nest survival increases in landscapes composed of more grassland (Greenwood et al. 1995, Reynolds et al 2001, Stephens et al. 2005). Likewise, the amount of habitat edge may influence predator foraging activity (Clark et al. 1999, Chalfoun et al. 2002, Phillips et al. 2003) and thus nest survival (Johnson and Temple 1990, Lahti 2001, Howerter 2003), although in potentially non-linear ways (e.g., Stephens et al. 2005).

1.4 Research objective and dissertation organization

The primary objective of this research is to test the correspondence of patterns in pintail habitat selection at multiple scales with predictions based on evolutionary theory and landscape ecology. A second objective is to use information about patterns of pintail habitat use and reproductive success to develop applied models for conservation planning.

Specifically, this work will examine multiple hypotheses regarding pintail habitat use relative to expected gradients in reproductive success from nest to landscape scales. Gradients in components of fitness across scales generally relate to the interaction of population density and landscape features and fragmentation that previous evidence indicates may affect reproductive success. I will use data from several regional field studies of nesting ducks, and long term continental-scale annual surveys, to test predictions about pintail selection of nest sites, habitat patches, and landscape attributes relative to expected fitness gradients. The results of this work will be used to create predictive models that include nest survival and habitat preference relationships that best fit the existing data.

In Chapter 2, I use pintail nest data collected from three multi-year waterfowl nesting studies conducted in prairie Canada by Ducks Unlimited Canada to first examine patterns of nest survival as a fitness metric relative to nest and patch-level covariates. Covariates measured at the landscape scale (e.g., pintail population density, percent cropland in the landscape) are included here to examine hypotheses regarding density-dependent effects and cross-scale interactions. I subsequently test whether factors affecting nest survival affect nest site and patch-level selection in the manner predicted by theory, including the existence of disruptive cues that could produce maladaptive habitat choice.

In Chapter 3, I use long-term waterfowl and hunter survey data to test alternate hypotheses to explain pintail selection of landscapes within the PPR. I first examine whether annual estimates of pintail recruitment (young/adult ratio in the fall harvest) are explained by covariates describing pintail distribution relative to landscape attributes within the PPR. I use 48 years of data from the May Waterfowl Breeding Population and Habitat Survey (MWBPHS; U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987), and hunter-killed birds collected from across the United States and Canada as part of the annual Parts Collection Survey (Couling et al. 1982, Geissler 1990). I then examine pintail habitat associations among landscapes within the PPR for correspondence with covariates explaining patterns in recruitment indices. Hypotheses relating fitness and landscape selection to wetland abundance, dominant land use, landform, geographic location, PPR pintail population size, and selected interactions of these factors are examined.

In Chapter 4, I integrate information from models developed during analyses conducted in Chapters 2 and 3 to construct 1) a GIS-based model of long-term average pintail distribution and abundance within the PPR, and 2) a deterministic model to predict prairie pintail reproductive success (e.g., Johnson et al. 1987) given landscape-level population size, habitat availability, estimates of nest habitat preference, nest survival, breeding season survival, and nesting and renesting effort (the latter 3 estimates from the literature). This will enable me to achieve my second broad research goal of linking theory with empirical findings to advance and improve conservation planning through integrated models, generally for animals, and specifically for pintails.

Finally, in Chapter 5, I synthesize my findings from evolutionary ecology and conservation biology perspectives with a focus on the role of scale in habitat selection decisions.

CHAPTER 2. ADAPTIVE HABITAT SELECTION IN RESPONSE TO PREDATION: NORTHERN PINTAIL NEST SURVIVAL AT NEST, PATCH, AND LANDSCAPE SCALES

2.1 Introduction

Theory suggests that animals should respond to variation in the availability of resources in space and time (e.g., migration, food-caching, nomadism, nest site selection) such that patterns of resource use reflect underlying variation in fitness as measured by survival or reproductive success (Rosenzweig 1974, Southwood 1977, Orians and Wittenberger 1991). Thus, in the absence of disrupting cues, high nest or population density (use) may be expected across scales where expected fitness is high. Because *a priori* knowledge about actual fitness among habitats is typically unavailable, individuals presumably have evolved the ability to identify proximate habitat cues that reliably reflect fitness at scales that are important (e.g., Martin 1998, Morris and Davidson 2000). Across species and taxa, however, evidence for adaptive habitat choice is mixed (Milinski and Heller 1978, Mayhew 1997, Clark and Shutler 1999, Misenhelter and Rotenberry 2000, Arlt and Part 2007, Chalfoun and Martin 2007). Non-correspondence with theory in field studies may arise due to poor understanding and lack of control of alternate factors affecting habitat selection or fitness metrics, multiple vital rates affecting realized fitness, incomplete understanding of species natural history, and failure to account for response at different spatial scales (Mayhew 1997, Calsbeek and Irschick 2007, Chalfoun and Martin 2007).

Theory also fails in special cases where cues are disruptive; if species prefer nest sites or landscapes where fitness is low, or avoid sites or landscapes where fitness is high, ecological traps (e.g., Schlaepfer et al. 2002, Gilroy et al. 2011) or perceptual traps (Patten and Kelly 2010),

respectively, may exist. Regardless, individual response to fitness cues and realized fitness translate into habitat-mediated demographic processes that regulate natural populations (Pulliam 1996).

For many terrestrial species, fitness gradients are created by patterns of land use that affect vegetative structure, associated biota, and disturbance regimes at multiple scales (Opdam and Wiens 2002). Hence, reproductive success or survival may be related to one or more characteristics of the nest site, the habitat patch, or the surrounding landscape (e.g., Orians and Wittenberger 1991, Battin and Lawler 2006, Howerter et al. 2008). The effect of habitat fragmentation on birds has probably received the most scientific scrutiny (but see Debinski and Holt 2000). Elevated nest predation rates have been documented in small patches (e.g., Wilcove 1985, Howerter 2003), in association with habitat edges (Paton 1993, Lahti 2001), and in fragmented landscapes (e.g., Hartley and Hunter 1998). Patch and edge effects are generally attributed to predators foraging frequently near edges (Andrèn and Angelstamm 1988, Larivière and Messier 2000, Chalfoun et al. 2002, Phillips et al. 2003).

Across scales, it is expected that habitats are limited in the number of individuals they can hold and fitness will eventually begin to decline with increasing density (e.g., Fretwell and Lucas 1969, Brown 1969). Fretwell and Lucas (1969) postulated that, while individuals will initially select habitats that confer the highest fitness, thereafter density within and among patches would be adjusted so that all individuals experience similar fitness regardless of habitat choice (i.e., the "ideal free" distribution). By contrast, the "ideal-dominance" model proposes that dominant individuals limit density and maintain higher fitness by forcing subordinates into lower fitness habitats; consequently, fitness varies among habitats. Similarly, Brown (1969), building on the hypothesis of Kluyver and Tinbergen (1953), postulated a version of the ideal-dominance model

where patch density is limited and individuals are forced into habitats of lower quality at high population levels, producing lower overall fitness (e.g., Potts et al. 1980, Pulliam et al. 1992). Under the Brown model, preference for habitats of lower suitability will increase at higher population density (see also Rodenhouse et al. 1997).

Northern pintails (*Anas acuta*; hereafter, pintail) are migratory dabbling ducks well suited to evaluating predictions arising from habitat selection theory. Pintails breed in the greatest concentrations on the North American prairies, a landscape that has undergone dramatic alteration due to agricultural production. Pintails are unique among North American dabbling ducks in their nomadic wanderings in response to varying wetland conditions, and use of diverse nesting habitats, ranging from bare soil to thick vegetation (Johnson and Grier 1988, Austin and Miller 1995). Declining populations since the 1970s and persistently low populations have sparked concerns regarding the potential for detrimental interactions between land use, habitat selection, and reproductive success (Miller and Duncan 1999, Podruzny et al. 2002, Hebert and Wassenaar 2005).

Nest survival is frequently measured and used as a surrogate for reproductive success because this demographic rate has important ramifications for population growth rate (e.g., Hoekman et al. 2002, Nagy and Holmes 2004, Mattson and Cooper 2007). In ducks, nest survival varies at regional (Reynolds et al. 2001, Drever et al. 2004), landscape (Stephens et al. 2005), habitat patch (Klett et al. 1988, Howerter 2003), and nest scales (Gloutney and Clark 1997, Guyn 2001, Howerter 2003). Nest survival is likely an important determinant of habitat selection behaviour at these scales, assuming that habitat cues reliably signal expected benefits. However, evidence for reproductive advantages of nest habitat selection is mixed (e.g., Clark and Shutler 1999, Richkus 2002, Howerter et al. 2008).

My central objective is to test predictions arising from alternative hypotheses about how multi-scale patterns of pintail habitat selection are related to nest survival (Table 2.1). I use data from three long-term waterfowl nesting studies with large samples of pintail nests. I first establish nest, patch and landscape variables associated with pintail nest survival, and then examine whether patterns of habitat use correspond with predictions of adaptive habitat selection. Variables potentially affecting nest survival at all scales are identified from previous research and expert opinion, as explained below.

2.2 Hypotheses and Predictions

Several characteristics that vary at the nest scale have previously been linked to nest survival. Nest survival varies with clutch initiation date both within and among habitats (e.g., Greenwood et al. 1995, Emery et al. 2005). Increasing nest survival through the nesting season has been attributed to better nest concealment due to vegetative growth or increasing quantities of alternate prey (Klett and Johnson 1982). Thus, I predict that if nest survival among nest sites or patches varies with season, relative selection among nest sites and patches will reflect observed changes in nest survival.

Distance to a habitat edge is a common habitat fragmentation metric suggested to affect avian nest survival, with lower survival predicted for nests located closer to an edge; a result of predator affinity for edge habitats (Andrén and Angelstamm 1988, Lahti 2001). Evidence for edge effects on waterfowl nests is mixed. Horn et al. (2005) reported opposite nest survival trends with distance to edge depending on the amount of grassland in the surrounding landscape. Clark and Shutler (1999) found successful blue-winged teal (*Anas discors*) nests tended to be located further from habitat edges but the opposite trend was found for gadwall (*Anas strepera*). Howerter et al. (2008) found mallard (*Anas platyrhynchos*) nest survival increased with distance

from habitat edges, especially wetland edges; a result consistent with findings that several duck nest predators preferentially forage near wetland edges (Larivière and Messier 2000, Phillips et al. 2003). I predict pintail nest survival will increase with distance from habitat edges, or wetland edges specifically, and pintails will distribute nests further from habitat edges than expected by chance.

At the patch scale, differences in waterfowl nest survival among habitat (patch) types and sizes has been well established, although definitions of habitat can vary (e.g., Klett et al. 1988, Greenwood et al. 1995). Habitat type definitions in agricultural landscapes typically incorporate both vegetation and land use components and may include habitats of special management interest. Here, I use common agricultural landscape habitat definitions (Table 2.2) that, based on previous research with waterfowl nests, differ in expected nest survival (Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Howerter 2003, Devries et al. 2008a). In general, habitats that provide greater concealment of the nest (e.g., idle grassland) tend to have higher survival than in habitat with lower nest concealment (e.g., spring-seeded cropland; Klett et al. 1988, Greenwood et al. 1995; but Devries and Armstrong 2010).

Larger habitat patches can have higher nest survival than small patches, likely as a result of reduced predator foraging efficiency, although the relationship can be nonlinear and habitat dependent (Sovada et al. 2000, Howerter 2003, Horn et al. 2005). I predict that nest survival will differ among habitats and patch sizes and that habitats with higher nest survival, and larger patches, will be preferred, while controlling for possible nonlinear and habitat-specific relationships.

I further predict that nest survival will vary with several covariates measured at a landscape scale. I define landscape scale as a regional scale that encompasses many different habitat patch types that, given the mobility of pintails, can be assumed 'accessible' once a female has settled to breed. I further assume that the size of the study areas examined in this study (~41 km^2; see below), approximates this landscape scale. Landscape-level covariates I examine are pintail breeding pair density, density of other breeding ducks, predominant land use, and wetland abundance.

I predict that nest survival will decrease with increasing pintail pair density given both field-scale and population-level evidence of density-dependent recruitment (Weller 1979, Johnson et al. 1997, Larivière and Messier 1998, Runge and Boomer 2005; but see Ackerman et al. 2004, Ringelman et al. 2012). Likewise, interactions with other duck species may affect fitness either through competition for space and resources or via a functional response where all avian/duck nests are collectively perceived by predators as the 'prey' (Cody 1981, Nudds 1983, Ims 1990, Robinson and Terborgh 1995, Nummi and Väänänen 2001, Elmberg et al. 2003, Gurd 2008). I predict a linear decline in nest survival with the breeding density of other ducks if competition is the mechanism, but predict lowest nest survival at moderate density of other species if predator swamping mediates the relationship between nest density and predator foraging responses (Ims 1990). Alternatively, pintails may cue on the presence of other species as indicators of landscape quality (Danielson 1992, Nudds 1983) leading to a prediction of higher nest survival in landscapes with high duck density.

Several studies have indicated that landscape composition affects nest survival. The amount of cropland or grassland (negatively correlated metrics) at landscape scales can affect the distribution of duck nests and the composition and foraging efficiency of nest predators

(Sargeant et al. 1993, Sovada et al. 2000). Generally, waterfowl nest survival increases with the amount of grassland and decreases with the amount of cropland (Greenwood et al. 1995, Reynolds et al 2001, Stephens et al. 2005). Mechanisms for this relationship likely relate to differences in predator communities that result in greater predation pressure and efficiency on nests in cropland-dominated landscapes than in grassland-dominated landscapes (Sargeant et al. 1993, Sovada et al. 2000, Gehrt and Clark 2003). For example, Phillips et al. (2003) noted shifts in skunk (*Mephitis mephitis*) and red fox (*Vulpes vulpes*) foraging pattern, and waterfowl nest survival, in high versus low grassland landscapes; foraging efficiency was likely diluted, and nest survival was higher, in high grassland landscapes. Changing predation pressure with changing landscape composition may change the relative benefits of specific habitat use as proposed by Mysterud and Ims (1998; i.e., a 'functional response' where habitat preference changes with habitat availability, see also McLoughlin et al. 2010). Thus, I predict that as cropland increases (or grassland decreases), nest survival and selection among habitats may change; for example, idle grassland will have lower nest survival and preference in high cropland landscapes.

Given evidence of wetland edge effects (above) and associations between predator foraging and wetland habitats (Greenwood et al. 1999, Larivière and Messier 2000, Phillips et al. 2003), it is plausible that nest survival would be lower in landscapes where wetland abundance, and hence wetland edge density, is high. If nest survival is reduced by wetland edge density at the landscape scale, I would predict a selection response primarily among landscapes rather than among habitats within a landscape (addressed in Chapter 3).

Given previous demonstration of differences in waterfowl nest survival among nest site and patch covariates, I predict that pintails will not follow an ideal-free distribution. Rather, existing

information suggests that the ideal-dominance distribution will be supported; sites or patches with higher nest survival will be preferred, and preferences may weaken at high population density (buffer effect).

Alternatively, it is plausible that pintails may experience an ecological trap (Schlaepfer et al. 2002) if they prefer to nest in cropland (where nest success is low) as hypothesized by Miller and Duncan (1999). Richkus (2002) concluded that pintails select habitat in proportion to availability but did not search all habitats equally. Avoidance of high nest survival habitats may indicate perceptual traps (Patten and Kelly 2010) but no existing evidence suggests this may be the case for pintails.

2.3 Study Area and Methods

2.3.1 Study Area

Data were obtained during three multi-year nesting studies conducted in prairie Canada by Ducks Unlimited Canada (DUC; PHJV Assessment Study, 1993–2000; Pintail Study, 2005–2007; Spatial/Temporal Variability Study [SPATS] 2001–2011), collectively designed to inform and improve delivery of habitat conservation programs. PHJV Assessment Study areas were single sites, 64 km^2 in size, and duck nesting ecology was studied at these sites for 1 year only (Howerter et al. 2014). Pintail Study and SPATS designs include clusters (hereafter, site-clusters) of 6 – 41 km^2 study areas stratified by percent grassland composition; 2 replicates each of low (< 30%), moderate (30-60%), and high (>60%) grassland area. Each site-cluster was examined for 1 or 2 years. From all studies, I include only sites, or site clusters, where ≥ 20 pintail nests were found per year. In total, 10 site clusters and 3 PHJV sites, representing 62 study areas (1997–2009), were included.

Most study areas were located in the grassland ecoregions (Fescue, Mixed, and Moist Mixed Grasslands) of Alberta and Saskatchewan but 3 study areas were located in the Aspen Parkland ecoregion (Figure 2.1; Ecological Stratification Working Group 1995). The climate across sites was humid continental with mean July temperatures ranging from 16.2° C in Calgary, Alberta (114°01' W, 51°06' N) and 18.2° C in Saskatoon, Saskatchewan (106°43' W, 52°10' N), to 18.5° C in Regina, Saskatchewan (104°34' W, 50°24' N); annual precipitation averaged from 413 mm (31% as snow) at Calgary and 350 mm (28% as snow) at Saskatoon, to 378 mm (22% as snow) at Regina (Environment Canada 2000).

Study areas were characterized by flat to hummocky or kettle topography formed by lacustrine deposits and deposition of glacial till (Ecological Stratification Working Group 1995). Because these studies were focused on finding duck nests, study area locations generally were randomly selected within regions of moderate to high amounts of wetland habitat in the form of ponds and shallow lakes (Stewart and Kantrud 1971, DUC unpublished data). Among study areas, wetland habitat averaged 12.7% (range: 4–39%) of the area within study area boundaries.

Primary land uses included cropland (predominantly for cereal grain and oil-seed production), and introduced and native grass forage lands (pasture and haylands) for cattle production. Native pasture and areas not in agricultural production were dominated by native grasses and shrubs with few trees (Ecological Stratification Working Group 1995). Approximately 99% and 92% of native and tame grasslands, respectively, were used as pasture and generally provided sparse cover throughout the nesting season. Haylands provided sparse cover early in the season but dense cover by early June (e.g., McMaster et al. 2005). Ungrazed and unhayed native and tame grasslands generally provided dense cover throughout the nesting season. Croplands included standing stubble of cereal crops (e.g., wheat, barley) and canola or

bare dirt (previous year's fallow land). Because winter cereal crops (fall rye, winter wheat) were of specific interest during the Pintail Study, these crops were seeded by DUC on study areas in September of the year prior to research activities. Location of fall-seeded crops within the study area boundaries was constrained by the willingness of producers to be involved in the study. All croplands provided sparse cover early in the nesting season although winter cereal crops included germinated seedlings in stubble in April and became relatively tall and dense by early June (Devries et al. 2008a). Research protocols among study sites were similar except that not all habitat types are represented in all studies (e.g., fall-seeded crops primarily examined in the Pintail Study).

2.3.2 Breeding pair surveys

Ground-based duck counts (Dzubin 1969a, Hammond 1969) were conducted at least twice on all study areas to estimate breeding pair densities for both early and late-arriving species. Early surveys occurred during late April-early May (for mallard and pintail), and late surveys occurred in late May (for other duck species). Generally, surveys were completed between 0800 and 1400 hours. Surveys were postponed during periods of high winds, fog, heavy rain or other low visibility conditions.

On PHJV Assessment sites, all wetlands within six non-overlapping 2.6 km^2 strip transects spanning the study area were surveyed (among-site range: 1.8–2.7 km^2 wetland area surveyed). Pair estimates were based on the average of 2 counts conducted on consecutive days for the early survey and on one count in late May for the late survey. On Pintail Study areas, bi-weekly roadside surveys (Sauder et al. 1971, Austin et al. 2003) counted waterfowl on wetlands within 200 m of all roads within 1.6 km of study area boundaries (0.5–1.7 km^2 wetland area). Early pair estimates were based on the average count of first and second surveys, and late pair estimates

were based on the average count of second and third surveys. On SPATS study areas, all wetlands within eight randomly selected quarter sections (0.2–2.6 km^2 wetland area) were surveyed, and estimates obtained, from single counts during early and late periods (above). Estimation of indicated breeding pairs followed Dzubin (1969a) and pair densities expressed as indicated breeding pairs/km^2 of wetland area surveyed. While both roadside and walking pair counts were conducted among studies, both methods are expected to provide similar results (Pagano and Arnold 2010).

2.3.3 Locating and monitoring waterfowl nests

Among studies, 3 or 4 nest searches were conducted at 3-week intervals from late April through mid-July following the procedures of Klett et al. (1986). Nests were found by dragging a 30 m cable-chain assembly or a 2.5 cm x 75 m rope between 2 all-terrain vehicles (ATV) through habitats being searched (Higgins et al. 1977). The ATV rope-drag was typically used in growing crops to minimize damage. Where ATV use was not practical, a 1 cm x 30 m rope was dragged between observers on foot, or lone observers walked and struck vegetation with willow switches to flush female ducks from nests. A nest was defined as a nest bowl with ≥ 1 egg attended by a female when found (Klett et al. 1986). Nest searches were conducted 6 days per week between 0700 and 1300 hours when most laying and incubating females are expected to be at nests (Gloutney et al. 1993). Searches were suspended during heavy rain. All habitat types were searched except growing crops if permission was denied by the landowner, trees, and flooded wetland vegetation. All areas searched were recorded on aerial photographs and later digitized in ArcGIS (ArcMap; ESRI, Redlands, CA).

When a nest was discovered, the habitat patch type, duck species, and number of eggs were recorded and incubation status was determined by field candling (Weller 1956). Nest location

was determined using GPS for later analyses in ArcGIS and nests were marked with a flagged willow stake placed 4 m north of the nest to facilitate relocation. Nests were revisited at 7–10 day intervals until nest fate (successful, failed, or abandoned) was determined. If the scheduled revisit was within 2 days of estimated hatch, we revisited the nest 2–3 days after the estimated hatch date to avoid separating the female from recently hatched ducklings. A successful nest was defined as hatching ≥ 1 egg as indicated by the presence of shell membranes (Klett et al. 1986) or ducklings in the nest bowl. Failed nests were indicated by evidence of abandonment or predation. When nests were abandoned on the first revisit following discovery (i.e., hen absent and no change in number of eggs or incubation), abandonment was attributed to investigator activity.

Clutch size was estimated by the number of eggs present on the first visit with evidence of incubation. However, where evidence of partial predation or nest parasitism was present, clutch size was indeterminate. I excluded from nest survival calculations nests that were abandoned due to investigator disturbance, fully or partially destroyed by investigators, or could not be relocated, but I included these nests in estimation of nest habitat preference. Clutch initiation date was estimated by subtracting the age of the nest when found (i.e., number of eggs plus days of incubation) from the date of discovery (Klett et al. 1986).

Research protocols for handling and disturbing birds and nests were approved by the University of Saskatchewan Animal Care Committee protocol #92007 (PHJV Assessment Study), Manitoba Wildlife Animal Care Committee (MWACC) permits #2002-05 and #2007-02 (SPATS Study), and MWACC #2005-01 (Pintail Study). Disturbance and handling of migratory waterfowl nests and eggs was permitted under Canadian Wildlife Service Scientific Permits WS-

M39 and CWS00-M004a (PHJV Assessment), CWS02-M006 (SPATS Study), and CWS05-S001 (Pintail Study).

2.3.4 Habitat classification and digitizing

I used a 6-class habitat definition scheme to describe a combination of vegetative and land-use characteristics typically used in many waterfowl nesting studies (e.g., Klett et al. 1988; Table 2.2). Habitat types were digitized in ArcMap from several imagery sources. During the PHJV Assessment study, 1:5,000 black-and-white infrared aerial photos taken in July or August of the year of investigation were used. On Pintail Study sites, 2.5 m panchromatic SPOT images (SPOT Image Corporation, Chantilly, VA) taken in May or June of the previous year were used. On SPATS study areas, 1:10,000 color or black-and-white infrared aerial photos taken in June-August of the year of investigation were used. All habitats within study area boundaries were ground-truthed in June and July of the year of investigation. I used ArcMap to extract various nest, patch, and landscape habitat covariates from the digitized habitat layers for use in analyses (e.g., Figure 2.2).

2.3.5 Nest survival analysis

I used a general likelihood specification in PROC NLMIXED to examine the influence of covariates on nest survival probability (Emery et al. 2005) and used a logistic link function to model daily survival rate (DSR) as a transformably linear function of covariates (Dinsmore et al. 2002). I included the random effect of study site or site-cluster to account for unmodelled differences in DSR among years and geographic locations.

First, I assembled covariates that potentially explained variation in pintail nest survival, selected on the basis of previous research and plausible hypotheses (described above). Then, I

constructed sets of *a priori* model suites containing covariates of potential importance at nest, habitat patch, and landscape scales. Where separate covariates measured related phenomenon (e.g., landscape-scale percent grassland is negatively related to percent cropland), or where covariates were correlated ($r > 0.5$), I included them separately in competing models. Full models included additive covariate main effects and selected within- and between-scale interactions that seemed plausible or tested specific hypotheses. I used Akaike's Information Criterion (AIC) adjusted for overdispersion ($\hat{c}$ = Pearson χ^2 / df, McCullagh and Nelder 1989; QAIC, Burnham and Anderson 2002) to assess model fit. Prior to full model construction, all continuous covariates were run singly and in their quadratic form, and the best fitting form (lowest QAIC) was used in full models.

I sequentially reduced full models using backward elimination of least predictive covariates (based on p-values) while maintaining model hierarchy. Top models from each scale were combined to create a full multi-scale model which in turn was reduced by backward elimination to arrive at a final best-fitting model. In all backward elimination procedures, I identified best-approximating models when elimination of additional covariates achieved no further reduction in QAIC (Burnham and Anderson 2002). I present models within 2 QAIC units of the best-ranked models, and among ranked models, I considered only structurally simpler models as competitors for drawing inference (Burnham and Anderson 2002, Arnold 2010). I used relative AIC weights (w_i) as a measure of support for each model.

Nest-level covariates included nest age (NSTAGE) in days, clutch initiation date (IDATE), and distances (m) to nearest wetland (DISTWET) and habitat (DISTEDG) edges (Livezey 1981, Guyn 2001, Dinsmore et al. 2002, Howerter 2003, Emery et al. 2005, Stephens et al. 2005). I standardized IDATE by study site or site-cluster ($\bar{x} = 0$, SD = 1) to account for annual/location

effects on this variable. DISTWET and DISTEDG were positively skewed and were square-root transformed to improve normality.

Two habitat patch scale variables were considered: habitat type (HAB; Table 2.2) and patch size in hectares (PATCHSZ), based on previous support for their influence on DSR (Klett et al. 1988, Greenwood et al. 1995, Sovada et al. 2000, Howerter 2003, Stephens et al. 2005). I considered five landscape variables measured at the scale of the study area (i.e., 41–64 km^2). To examine the influence of intraspecific density dependence on nest survival (e.g., Weller 1979), I included the density of breeding pintail pairs (PINDEN). To examine interspecific density dependence through putative mechanisms such as food competition or functional predator response (e.g., Minot 1981, Ims 1990), I included the density of all breeding duck pairs (DUCKDEN) except pintails. Percentages of the landscape composed of cropland (PCTCROP) and grassland (PCTGRASS; i.e., all grass types plus hayland) were included as alternate variables indicating the intensity of agricultural use and potential predator community composition (Greenwood et al. 1995, Sovada et al. 2000, Stephens et al. 2005). Finally, I included wetland edge density (WEDGDEN; km of wetland edge/km^2 of study area; Larivière and Messier 2000, Howerter 2003). To improve normality, PINDEN was transformed with a square-root transformation and WEDGDEN was transformed with a natural log transform prior to analysis.

I included within and among scale interactions that seemed biologically plausible. Specifically, at the nest site scale, I included an interaction between IDATE and DISTWET (or DISTEDGE) examining potential within-season variation in distance to edge effects. At the patch scale, I included an interaction between HAB and PATCHSZ recognizing that patch size effects may vary with habitat type. At the landscape scale, I included interactions between

PCTGRASS (or PCTCROP), PINDEN, and DUCKDEN examining the potential of landscape composition to moderate density effects. Contingent on the results of within-scale model reductions, I included among-scale interactions HAB*IDATE, HAB*PCTCROP, and HAB*PINDEN to test whether season, landscape composition, or pintail density effects on DSR varied among habitat types.

2.3.6 Habitat selection analysis

I used covariates retained in competing nest survival models as a basis for constructing habitat selection models and testing central predictions of an adaptive selection hypothesis. Specifically, I used resource selection functions (RSFs; Manly et al. 2002, McLoughlin et al. 2006, 2010) to examine the influence of covariates affecting nest survival on pintail habitat use versus availability. RSFs are useful for inferring preference based on departures from random use while considering covariate effects that can provide insight into underlying ecological processes (McLoughlin et al. 2010). I used logistic regression (PROC GLIMMIX, SAS Institute; e.g. Gillies et al. 2006) to compare the distribution of used versus random locations among habitats at the scale of the study area. Specifically, I compared the observed distribution of nest sites among habitats (coded as 1's) with a sample of 300 points (coded as 0's) distributed randomly among all habitat patches within a study area. Both nests and random points were constrained to include only those in habitat patches where at least three complete nest searches had been conducted. To account for the clustered data structure I specified random intercepts at the study area level. Among study areas, 897 pintail nest sites and 17,895 random points were included in the analysis.

I began with a full model examining selection ratios among HAB categories and including interactions of HAB with each variable influencing nest survival from the best-fitting nest

survival model. Random points were assigned patch and study area level covariate values based on location. I converted IDATE to a categorical variable (IDAT3CAT) for nests and assigned early, mid, and late initiations based on 33rd percentiles, and I randomly assigned one third of random points to each IDAT3CAT category. To further examine selection relative to the seasonal pattern observed in nest survival, I included an alternate two category IDATE variable (IDAT2CAT) contrasting mid-season versus early- and late-season combined. I included PCTCROP and PCTGRASS in alternate full models because it is plausible that agricultural intensity could impact nest selection patterns without affecting nest survival directly (i.e., functional response; Mysterud and Ims 1998).

To directly examine the relationship between habitat selection and fitness, I included a set of full models where categorical HAB was replaced with habitat-specific estimates of DSR (HAB_DSR) from the nest survival analysis. The best-fitting full models from the HAB and HAB_DSR model sets (by AIC, $\hat{c}$ = 0.95) were then reduced by backward elimination to arrive at a best fit model given the data. To assess the fit of best-approximating models, I plotted the Receiver Operating Characteristic (ROC) curve, and report the area under the curve (AUC) which provides a measure of model performance for binary response models.

In nest survival and habitat selection analyses, I present models within 2 AIC units of the best-approximating models, and among ranked models, I considered only structurally simpler models, or models containing alternate variables, as competitors for drawing inference (Burnham and Anderson 2002, Arnold 2010). In all model suites examined, I included a NULL model that incorporated intercept and random effects terms. I present model-averaged means and effect estimates (±1 SE) based on top-ranked models. I report DSRs and observed nest survival (i.e., percent of nests that hatch; = DSR^{32} x 100) based on the average nest age (32 days) at hatch for

pintails (Klett et al. 1986). Habitat preference results are reported as relative selection ratios based on the nest:random point ratio I used. I report 85% confidence limits to be consistent with information theoretic approaches (Burnham and Anderson 2002, Arnold 2010).

2.4 Results

Among studies, pintail nest searches were conducted on a total of 24,682 ha of habitat (among study area range: 126–2,044 ha). Pintail nests comprised 1,005 of 9,038 nests found; 927 and 897 pintail nests were used in nest survival and habitat selection analyses, respectively. Covariate values varied widely at nest, patch and landscape scales (Table 2.3).

2.4.1 Nest Survival

Across scales, I examined 43 models relating pintail nest survival to covariates at nest, patch, and landscape scales (Appendix A). The best-approximating models of DSR at the nest scale included the quadratic form of IDATE, and DISTWET (Table 2.4). At the patch scale, the best-approximating model contained only HAB. At the nest and patch scales combined, the best-approximating model contained the quadratic form of IDATE, HAB, and a HAB*IDATE interaction. At the landscape scale, competing reduced models comprised PINDEN, PCTCROP, the quadratic forms of DUCKDEN and WEDGDEN, and a PINDEN*PCTCROP interaction (Table 2.4). Variables in the best-approximating and competing models from the above scale combinations were combined into a multi-scale full model for final model reduction (Table 2.4).

Among multi-scale reduced models, the best-approximating model of nest DSR included HAB, PINDEN, and the quadratic form of IDATE ($w_i = 0.24$; Table 2.5). Alternate models within 2 QAIC units included the quadratic forms of DUCKDEN and WEDGDEN, PCTCROP and the PCTCROP*PINDEN interaction, and a HAB*IDATE interaction. Given relatively low

model weights among these models, I model-averaged effect estimates and standard errors (Table 2.6) but present DSRs as estimated from the highest ranked model containing each parameter. Based on effect estimates, the HAB*IDATE and WEDGDEN effects are weak (Table 2.6) and were not considered further.

The best-approximating model indicated that DSR varied from 0.907 (± 0.023; 4.4% nest survival) in wetland margins to 0.968 (± 0.007; 35.6% nest survival) in fall-seeded cropland (Figure 2.3). DSR declined as the density of pintail increased (Figure 2.4) and exhibited a non-linear relationship with clutch initiation date such that nest survival was highest for mid-season clutch initiations (Figure 2.5). Alternate models suggested that DSR was influenced by the density of other ducks such that nest survival was lowest at mid-range duck density (Figure 2.6). Further, alternate models indicated that pintail density and landscape composition interact such that nest survival declines with percent cropland at low to moderate pintail density (Figure 2.7) and the pintail density effect was stronger in landscapes with less cropland (Figure 2.8). Nest survival was uniformly low at high pintail densities and in highly cropped landscapes (Figs. 2.7, 2.8).

2.4.2 Nest Habitat Selection

I began with eight full habitat selection models including various combinations of HAB and habitat-specific DSR (HAB_DSR) interacting with alternate covariates identified in nest survival models. Among full HAB and HAB_DSR model alternatives, the best-approximating models of selection ratios in each suite included effects of IDAT3CAT, PINDEN, DUCKDEN, and PCTGRASS (Appendix B).

The best-approximating model of selection probability ratios included interactions between HAB and each of IDAT3CAT, PINDEN, and PCTGRASS ($w_i = 0.82$) and no competing models

were identified within 2 AIC units (Table 2.7). Under this model, preference within habitat categories varied among early, mid, and late clutch initiations. Idle grassland, hayland during mid and late season, and fall-seeded crops during late-season were preferred. Fall-seeded croplands early in the season, grazed grasslands during mid and late-season, and spring-seeded croplands during late-season were avoided. Spring-seeded cropland was used in proportion to its availability in early and mid-season as was fall-seeded cropland during mid-season. Wetlands tended to be avoided throughout the nesting season (Figure 2.9). Habitats with highest nest survival all trend toward being preferred habitats by late-season, most notably for fall-seeded cropland (Figure 2.9).

Selection ratios among habitats varied with PINDEN; however, this relationship was primarily driven by an increasing preference for cropland and hayland as PINDEN increased (Figure 2.10). Likewise, the influence of PCTGRASS was driven by stronger preference for spring cropland and grazed grasslands as PCTGRASS increased (Figure 2.11). The AUC for this model (0.823) indicates very good discrimination between nest sites and random points.

The best-approximating HAB_DSR model ($w_i = 0.64$) incorporated the same covariates as the HAB model although model fit was inferior (Table 2.7). Nevertheless, this model indicated a positive relationship between habitat-specific DSR and preference, most notably increasing as the nesting season progressed (Figure 2.12). Furthermore, the strongest relationship between preference and habitat-specific DSR occurred when population density was low (Figure 2.13) and in landscapes with low amounts of grassland (higher cropland; Figure 2.14). At average continuous covariate values and applying equal weight across initiation date categories, this model estimates a strong positive relationship between preference and habitat-specific DSR (Figure 2.15). Model fit as indicated by AUC (0.818) was similar to the top HAB model.

2.5 Discussion

My results provide strong evidence that avian fitness varies in time and space and that correspondence in patterns of nest habitat preference suggest that nest habitat preferences are adaptive. Preferences were generally weak for habitat with low nest survival (croplands, wetlands) and strong for habitats with high nest survival (fall-seeded cropland, idle grassland). Correspondence between preference and nest survival increased during the nesting season suggesting a within-season response to a seasonally varying cue. When viewed through the lens of nest survival as the fitness metric, nest habitat selection in pintails generally does not conform to a central prediction of the ideal-free distribution; individuals clearly experienced differences in nest survival among habitats. Rather, this observation supports the ideal-dominance distribution. Further, evidence of overall greater preference for habitats with higher nest survival, but declining expression of preference with population density, is consistent with the ideal-dominance distribution as presented by Brown (1969).

Despite this support, pintails do not exhibit clear dominance hierarchies or dominance-related behavioral interactions during the process of nest site selection, leaving the displacement mechanism somewhat speculative. Female pintails, like other ducks, are subject to intense harassment by paired and unpaired males at high breeding densities (Smith 1968, Derrickson 1978, Titman and Lowther 1975). It is plausible that older females, or females in better condition, are more able to avoid or cope with harassment, and thus occupy preferred habitat at high density. This could explain Kowalchuk's (2013) observation that older female pintails tended to occupy grassland-dominated landscapes while younger females occupied less-suitable cropland-dominated landscapes. Thus, the ability of female pintails to cope with harassment by males may provide a more plausible explanation than simple dominance as the dispersing

mechanism. Dispersal may be accentuated if yearling females comprise a greater proportion of the population in years when populations are high.

Correspondence between theory and observation in the examination of adaptive habitat preference is uncommon (Martin 1998, Chalfoun and Schmidt 2012). Failure to find correspondence in other studies has been attributed to examination of inappropriate scales of habitat selection, measurement of inappropriate fitness metrics, or misidentification of important habitat components (Arlt and Part 2007, Chalfoun and Martin 2007). The results presented here are based on a large sample of pintail nests found over multiple years, across a wide geographic region of prairie Canada, in a variety of landscapes available to breeding pintails. In addition, the analyses include covariates at multiple scales, and uses a robust metric of fitness in birds (nest survival; Martin 1993, Hoekman et al. 2002, Chafoun and Martin 2007). Unlike many previous studies of habitat selection in ducks, this study invested equal effort in searching active cropland, a dominant habitat type used by nesting pintails (e.g., Devries et al. 2008a). Ducks are a good model for examination of nest site selection because large samples of nests are usually available, nest sites are readily characterized by site and habitat characteristics, and a wealth of studies have described habitat selection; ironically, however, few studies have placed duck nest site preferences in an adaptive context (Clark and Schutler 1999).

Clark and Schutler (1999) encouraged researchers to first identify the fitness consequences of habitat choice as an indicator of natural selection processes that predict patterns in habitat use. Selection of nest sites, especially in ground-nesting birds, has important ramifications for reproductive success given the vulnerable nature of nests and potential risks to attendant parents (Martin 1993, Newton 1998). Thus, we expect natural selection to have shaped nest site preferences to a degree correlated with the risks among choices. In my analysis, an important

assumption was that nest survival is a primary component of pintail fitness, and a driver of selection behaviour among nest habitats. In making this assumption I recognize the potential of other vital rates to impinge on the selection process; for example, the consequences to adult or duckling survival of nest site decisions (Chalfoun and Schmidt 2012). I feel this assumption is reasonable given the disproportionate importance of nest survival versus other vital rates in the population growth potential in many bird species (Ricklefs 1969, Martin 1993, Hoekman et al. 2002).

For northern pintails, use for nesting and nest survival within croplands is of special interest given a prevailing view that selection of nest sites in spring-seeded cropland, and subsequent nest destruction by agricultural practices, is a primary cause of their declining populations in North America (Miller and Duncan 1999, Podruzny et al., 2002, Richkus 2002). My nest survival results were generally consistent with previous studies showing low nest survival in croplands (Higgins 1977, Klett et al. 1988, Greenwood et al. 1995, Devries et al. 2008a). Low nest survival in spring-seeded cropland is generally attributed to nest destruction by spring tillage/seeding and this has led to suggestions that spring-seeded cropland may be an ecological or evolutionary trap (Miller and Duncan 1999, Richkus 2002, Schlaepfer et al 2002). Approximately 25% of non-abandonment nest failures in spring-seeded cropland were the result of spring tillage in this study with the balance due to predation, a result similar to previous estimates (17%, Greenwood et al. 1995; 20–33%, Richkus 2002; 18%, Devries et al. 2008a). My results do not support spring-seeded cropland being an ecological trap; nest survival was indeed low in spring-seeded cropland, but this habitat was generally used in proportion to availability (early and mid-season nests) or avoided (late nests; Figure 2.9).

The relative selection of croplands in combination with the disproportionate availability of spring-seeded cropland across much of the PPR nonetheless suggests that a substantial proportion of the pintail breeding population may be exposed to relatively low nest survival in this habitat. Arguably, avoidance of cropland would be adaptive, however, given this is a relatively recent anthropogenic disturbance, or a novel habitat with characteristics similar to native prairie (i.e., short, low concealment cover through much of the pintail nesting season), lack of avoidance may represent an evolutionary trap (Schlaepfer et al. 2002).

Fall-seeded croplands (winter wheat, fall rye), on the other hand, could greatly benefit nesting pintails because these crops are generally undisturbed through the nesting season and typically have high nest survival (Duebbert and Kantrud 1987, Devries et al. 2008a, this study). Avoidance of fall-seeded cropland early in the nesting season may represent a perceptual trap (Patten and Kelly 2010) given this habitat has the highest nest survival of those examined. These crops are relatively rare in the Canadian PPR (more common in the U.S. PPR) and early in the growing season they are similar in appearance to spring-seeded cropland. Interestingly, fall-seeded cropland showed the largest change in selection through the nesting season, progressing from being avoided early to being preferred by late nesting pintails (likely renesters; Figure 2.9). Rapid and robust plant growth through the nesting season, and hence improving nest concealment potential, may cue greater nest survival in these crops.

Nest concealment differences among habitats may be a reliable cue for pintails. Idling grassland is a common management practice to increase waterfowl use and nest survival (e.g., Livezey 1981, Duebbert et al. 1981), and haylands can have relatively high nest survival when haying operations occur later in the nesting season (Klett et al. 1988, McMaster et al. 2005). In this study, habitats with greater concealment value (e.g., idle grass), or that typically improved in

concealment value through the nesting season (haylands, fall-seeded cropland) had higher nest survival and were all preferentially selected at some point in the nesting season. Nest concealment potential is a readily assessed cue and generally positively associated with habitat use in ducks (Crabtree et al. 1989, Devries and Armstrong 2010, Arnold et al 2007), although nest survival benefits may not be consistent (Schrank 1972, Devries and Armstrong 2010, Clark and Schutler 1999).

Haylands approached preference during the mid and late-season likely as a result of use by renesting females. While nest survival in haylands was generally high, female and nest mortality due to haying operations could contribute to a local ecological trap effect in some years if haying operations overlap the nesting period (e.g., Hoekman et al. 2006). In this study, approximately 16% of non-abandonment pintail nest failures in haylands were the result of haying operations.

Wetlands were avoided habitat consistent with the very low nest survival experienced in this habitat. This pattern reflects the findings of Klett et al. (1988) for pintails in North Dakota, and Greenwood et al. (1995; Appendix E, Table 2.5) for pintails in prairie Canada. The tendency for common predators of duck nests to concentrate foraging activity near wetlands likely drives this pattern (Larivière and Messier 2000, Phillips et al. 2003, Horn et al. 2005).

Nest success declined with increasing pintail population density in this study, a finding that, while consistent with a theory of density-dependent population limitation, is rarely reported in ducks or other birds. Population density did not interact with habitat suggesting that nest survival declines with density occurs uniformly across habitats. Few studies have reported density-dependent reproduction in waterfowl at the landscape scale (but see Weller 1979), but more have linked nest survival and nest density at the patch (field) scale, although the two may be correlated (Clark and Nudds 1991, Larivière and Messier 1998, Ackerman et al. 2004).

Plausible mechanisms linking breeding population density to nest survival include increased probability of predators finding nests as nest density increases (assuming population density and nest density are correlated; e.g., Weller 1979, Larivière and Messier 1998) and increased competition for food reducing nest attendance and increasing the probability of nest failure through discovery by predators, or abandonment (Drever et al. 2004, Drever and Clark 2007). Considering pintails alone, a predator response to pintail density seems unlikely. However, I found evidence that pintail nest survival was lowest at moderate aggregate densities of other resident ducks (Figure 2.6). This observation is consistent with the hypothesis that predators may cue on duck nests in aggregate at moderate densities (i.e., a functional response) but are swamped at high duck densities (e.g., Ims 1990, Larivière and Messier 1998).

Because there is little evidence that ground-nesting ducks compete for nest sites, except perhaps at unusually high densities (Lokemoen et al. 1984), pintails may be expected to select nest sites among habitats in an ideal-free manner (Fretwell and Lucas 1969). My findings that pintails ultimately experienced differing nest success among habitats is inconsistent with predictions of the ideal-free distribution. There was strong evidence of correspondence between preference and nest survival at low population density, but this weakened substantially at high population density where nest survival in all habitats was generally low. Hence, a general observation is that correspondence between preference and nest survival among habitats appears to weaken as population density increases (Figures 2.10, 2.13) and nest survival decreases in all habitats. A broad interpretation of this pattern is that benefits of selection may only be realized (and hence expressed), when the fitness differential among habitats is above a certain threshold (i.e., 1 vs. 2% nest survival doesn't matter, 10 vs. 20% does). These observations tend to support the prediction of Brown (1969, p.351) that "utilization of poor habitats becomes beneficial

mainly when rich habitats are near or past their own optimal densities or when the difference between rich and poor habitats is not large." Thus, I propose that selection may exhibit characteristics of ideal-dominance at low population density and ideal-free at high population density.

Consistent with previous research, there was evidence that nest success decreased with the amount of cropland in the surrounding landscape; however, the magnitude of this effect depended on pintail density. Decreases in nest survival with percent cropland were greatest at low pintail density, and decreases in nest survival with pintail density were greatest in low cropland landscapes (Figures 2.7, 2.8). Nest survival was uniformly lower in high cropland landscapes at all densities and at high pintail densities in all landscape compositions. This finding provides evidence that landscape composition mediates the density-dependent mechanism discussed above and hence the adaptive value of habitat selection. It follows that adaptive selection appeared to weaken and disappear as the amount of grassland in the landscape increased. This pattern was apparent in both the categorical habitat analyses and when habitats were defined by their nest survival; habitat preference was positively related to nest survival in landscapes with low to moderate areas of grassland but no relationship existed in high grassland landscapes (Figures 2.11, 2.14). This pattern was driven by a stronger preference for spring-seeded cropland and grazed grassland, and a weaker preference for idle grassland in high-grassland landscapes while preference for other habitats changed little (Figure 2.11). This is a good example, I believe, of a functional response in resource selection (sensu Mysterud and Ims 1998) whereby preference for a resource changes with the availability of a dominant habitat. Degradation of preference as the amount of grassland in the landscape increases signals a decreasing benefit to expressing preference, possibly in response to increasing nest survival in

the presence of a more benign predator community and larger patches of more suitable habitat (e.g., Sargeant et al. 1993, Sovada et al. 2000, Stephens et al. 2008).

Despite findings from previous nesting studies, I found equivocal evidence of habitat edge effects on pintail nest survival; when detected, effects were primarily associated with wetland edges. While distance from a nest to the nearest wetland was included in the top nest-level model of nest survival, the effect was marginal and this factor was not retained in subsequent models. Likewise, the quadratic effect of wetland edge density was retained in landscape-level and multi-scale models, but the effect was equivocal (Table 2.6). Nest survival was not associated with distance to an upland habitat edge, landscape-level habitat edge density, or patch size, so by these measures, habitat fragmentation appears to have little direct impact on pintail fitness. Therefore, I concluded that edge effects are unlikely to affect nest placement by pintails and did not consider these further in selection models.

My results show a strong nonlinear temporal effect of clutch initiation date such that nest survival was highest for mid-range clutch initiation dates. This pattern differs from previous reports for prairie pintails which have indicated increasing or no seasonal trend (Greenwood et al. 1995, Guyn and Clark 2000, Drever and Clark 2007) but trends can vary annually (e.g., Grant and Shaffer 2012). Nest survival of other dabbling ducks has shown opposing trends with clutch initiation date among habitats (e.g., Emery et al. 2005); however, lack of an interaction with habitat in my top models indicates this was not the case for pintails. Given the spatiotemporal span of my data and large sample sizes, I infer that the observed trend represents a generalized seasonal pattern of pintail nest survival in prairie Canada. Relatively poor nest survival for early nesting pintails presents a fitness tradeoff given clutch initiation date consequences for lifetime reproductive success (Kokko 1999, Drent et al. 2003). Early-hatched waterfowl tend to recruit to

breeding populations at higher rates than late-hatched young (Dzus and Clark 1998, Blums et al. 2002, Blums and Clark 2004), and early-hatching pintail ducklings survive better than do late-hatching individuals (Guyn and Clark 1999). Poor early spring nest survival was likely a result of generally poor vegetative concealment of nests and nest destruction by spring tillage. While early spring weather events can reduce pintail nest survival (e.g., Greenwood et al. 1995), no weather-related nest loss was documented in my study. The seasonally increasing, then decreasing, trend in nest survival may be due to seasonally increasing buffer prey abundance (e.g., Ackerman 2002) followed by predator switching to duck nests as late pintail nests generally coincide with peak nesting by other dabbling ducks (Greenwood et al. 1995).

In summary, this analysis provides strong evidence that pintails select nesting habitats adaptively but that the strength of habitat preference depends on population density and cropping intensity, factors that interactively reduce fitness across habitats. Ideal-free nest distribution was generally not supported; rather, my results support the ideal-dominance distribution of Fretwell and Lucas (1969) with important mediating effects of population density and dominant habitat availability as explored by Brown (1969) and Mysterud and Ims (1998). Further experiments are needed to clarify the mechanisms driving the observed interaction of fitness, population density, habitat availability, and habitat preference.

The results of this chapter address the fitness consequences of pintail selection among habitats available for nest placement once they have chosen to settle and breed in a specific location within the PPR. In keeping with the hierarchical nature of habitat selection in migratory birds, the following chapter addresses fitness consequences of selection among potential breeding locations within the PPR.

Table 2.1. Assumptions and predictions associated with five hypotheses at two scales (nest site and habitat patch). Predictions are associated with distribution models of Fretwell and Lucas (1969; Ideal-free and ideal dominance), Brown (1969; buffer effect), and ecological and perceptual traps (Schlaepfer et al. 2002, Patten and Kelley 2010). Models characterized as 'IDEAL' indicate that individuals select habitat that maximizes fitness. Models characterized as 'FREE' indicate that all individuals are equally capable of settling in all habitats.

	Nest Distribution Models				
	Fretwell-Lucas: Ideal Free	Fretwell-Lucas: Ideal Dominance	Brown: Buffer Effect[a]	Ecological Trap	Perceptual Trap
	IDEAL			NON-IDEAL	
	FREE	NOT-FREE		FREE	
General Assumptions	Nest survival is inherently different among sites and patches but nest survival decreases with use (i.e., density) at sites or within patches. Individuals are 'freely' distributed among sites and patches such that nest density is adjusted so all sites or patches have similar survival.	Nest survival is inherently different among sites and patches and is unaffected by use. Best sites or patches are preferentially occupied by dominant individuals, forcing subordinates into sites or patches where nest survival is lower.	Nest survival is inherently different among sites and patches and is unaffected by use. Site or patch occupancy is limited so that increases in population size result in higher use of sites or patches with lower nest survival.	Nest survival is inherently different among sites and patches. Cues reflecting habitat suitability are misleading.	Nest survival is inherently different among sites and patches and is unaffected by use. Individuals are unable to reliably detect cues that reflect habitat suitability.
Predictions: Nest site scale	Nest survival does not vary with site-level covariates (i.e., distance to edges).	Nest survival varies with site-level covariates; nest survival tends to be higher at preferred sites.	Nest survival varies with site-level covariates; preference for sites with low nest survival will increase with population density.	Nest survival varies with site-level covariates; sites with low nest survival are preferred.	Nest survival varies with site-level covariates; sites with high nest survival are avoided.
Predictions: Patch scale	Nest survival does not vary with patch-level covariates (i.e., habitat, patch size).	Nest survival varies among habitats and/or patch sizes; nest survival tends to be higher in preferred patches.	Nest survival varies among habitats and/or patch sizes; preference for patches with low nest survival will increase with population density.	Nest survival varies among habitats and/or patch sizes; patches with low nest survival are preferred.	Nest survival varies among habitats and/or patch sizes; patches with high nest survival are avoided.

[a] Brown's (1969) Buffer Effect distribution is a contemporary and similar hypothesis to the Fretwell-Lucas Ideal Dominance distribution, extended to predict density effects on population-level productivity. Thus, it includes predictions about the influence of population density on relative habitat preference but is similar to Fretwell and Lucas (1969) in terms of the underlying ideal-dominance mechanism.

Table 2.2. Description of habitat types (HAB) used in the analysis of pintail nest survival and habitat preference at study areas in Alberta and Saskatchewan 1997–2009.

Habitat type	Description
Spring cropland	Areas that are planted to grain or row crops in the spring, or that retain previous year's crop stubble and are fallowed (tillage or chemical) during the growing season.
Fall cropland	Croplands that are seeded and germinate in the fall, go dormant over the winter, and grow to maturity the following spring and summer (e.g., winter wheat and fall rye).
Grassland - idle	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs ≤ 30%) and have not been disturbed by haying, mowing, or grazing.
Grassland - grazed	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs ≤ 30%) that have been primarily disturbed by grazing (may contain some hayed or mowed lands but exclude lands specifically planted for hay-see Hayland).
Hayland	Areas that have been seeded to grass and/or legume mixtures for forage production and that are hayed annually.
Wetland	All areas, regardless of size, mapped as wetland according to definitions in Cowardin et al. (1979). Wetlands may be idled, grazed or hayed.

Table 2.3. Untransformed covariate statistics at nest, patch, and landscape scales for pintail nests found at study areas in Alberta and Saskatchewan 1997–2009.

Scale	Covariate	Mean (Median*)	Range
Nest (n=927)			
	IDATE	136	100–180
	DISTWET (m)	55*	0–444
	DISTEDG (m)	39*	0–333
Patch (n=289)			
	PATCHSZ (ha)	57.3*	0.2–3,158.0
Landscape (n=62)			
	PINDEN	23.2*	0–151.7
	DUCKDEN	157.5	27.7–348.5
	WEDGDEN	4.6*	2.5–16.5
	PCTCROP (%)	41.3	0–87.3
	PCTGRASS (%)	42.5	0.9–93.6

Covariates: IDATE – days since 1 January (e.g., 135 = May 15), DISTWET – distance to nearest wetland edge, DISTEDG – distance to nearest habitat edge, PATCHSZ – size of habitat patch containing the nest, PINDEN – Pintail pair density (pairs/km^2 surveyed wetland), DUCKDEN – Non-pintail duck pair density (pairs/km^2 surveyed wetland), WEDGDEN – wetland edge density (km wetland edge/km^2 study area), PCTCROP – percent of study area extents in annual croplands, PCTGRASS – percent of study area extents in grasslands (i.e., all grass types + haylands).

Table 2.4. Nest, patch and landscape scale models used to screen variables for inclusion in multi-scale full models examining variation in pintail nest survival at study areas in Alberta and Saskatchewan, 1997–2009. Multiple full models are presented at each scale where alternate covariates are present. Best-approximating models are presented based on lowest QAIC. Competing models (i.e., structurally simpler and/or containing alternate covariates than the top-ranked model; Arnold 2010) within 2 QAIC of the best-approximating model are labeled "Competing". Variables present in competing models are taken forward into the multi-scale full model for final model reduction. Note that because $\hat{c}$ (overdispersion index) differs between scales, QAIC values among scales are not comparable. The NULL model includes intercept and random effect terms for reference. A full list of models examined is provided in Appendix A. N refers to number of pintail nests.

Model	**Parameters[a]**	**QAIC**
Nest Level (n = 927, $\hat{c}$ = 1.13)		
Best-approximating: DISTWET + IDATE + IDATE^2	2	1703.3
Full 1: NESTAGE + DISTWET + IDATE +IDATE^2 + IDATE*DISTWET + IDATE^2*DISTWET	8	1703.3
Full 2: NESTAGE + DISTEDG + IDATE +IDATE^2 + IDATE*DISTEDG + IDATE^2*DISTEDG	8	1704.4
NULL	2	1703.3
Patch Level (n = 927, $\hat{c}$ = 1.24)		
Best-approximating: HAB	7	1530.8
Full: HAB + PATCHSZ + HAB*PATCHSZ	13	1531.5
NULL	2	1542.7
Nest+Patch Level (n = 927, $\hat{c}$ = 1.32)		
Best-approximating: IDATE + IDATE^2 + HAB + HAB*IDATE	14	1440.4
Full: DISTWET + IDATE + IDATE^2 + HAB + HAB*DISTWET + HAB*IDATE + HAB*IDATE^2	25	1451.1

Landscape Level (n = 929, $\hat{c}$ = 1.16)		
Best-approximating: PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + WEDGDEN + WEDGDEN^2 + PCTCROP*PINDEN	9	1641.8
Full 1: PINDEN + DUCKDEN + DUCKDEN^2 + PCTGRASS + WEDGDEN + WEDGDEN^2 + PCTGRASS*PINDEN + PCTGRASS*DUCKDEN + PCTGRASS*DUCKDEN^2	11	1647.2
Full 2: PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + WEDGDEN + WEDGDEN^2 + PCTCROP*PINDEN + PCTCROP*DUCKDEN + PCTCROP*DUCKDEN^2	11	1644.6
Competing 1: PINDEN + DUCKDEN + DUCKDEN^2 + WEDGDEN + WEDGDEN^2	7	1642.4
NULL	2	1652.1
Multi-scale Full Model (n = 929, $\hat{c}$ = 1.39)		
IDATE + IDATE^2 + HAB + HAB*IDATE + PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + WEDGDEN + WEDGDEN^2 + HAB*PINDEN + PCTCROP*PINDEN + HAB*PCTCROP	31	1382.1

[a] include intercept and random effects.

Table 2.5. Best-approximating models (i.e., within 2 Akaike Information Criterion [QAIC] units of the top ranked model), full models, and the null model from the multi-scale analysis examining pintail nest survival rate as a function of clutch initiation date (IDATE), habitat type (HAB), pintail pair density (PINDEN), non-pintail total duck pair density (DUCKDEN), percent cropland or grassland within study areas (PCTCROP, PCTGRASS), and wetland edge density (WEDGDEN) at study areas in Alberta and Saskatchewan 1997–2009. The NULL model includes only an intercept and random effect term for reference.

MODEL	**QAIC**	**Parameters**	**Δ QAIC**	**Model weight (w_i)**
IDATE + IDATE^2 + HAB + PINDEN	1365.4	10	0.0	0.243
IDATE + IDATE^2 + HAB + PINDEN + DUCKDEN + DUCKDEN^2 +PCTCROP + PCTCROP*PINDEN	1366.6	14	1.2	0.136
IDATE + IDATE^2 + HAB + PINDEN + PCTCROP + PCTCROP*PINDEN	1366.9	12	1.5	0.115
IDATE + IDATE^2 + HAB + HAB*IDATE + PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + PCTCROP*PINDEN	1366.9	19	1.5	0.115
IDATE + IDATE^2 + HAB + PINDEN + PCTCROP	1367.3	11	1.9	0.092
IDATE + IDATE^2 + HAB + PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + WEDGDEN + WEDGDEN^2 + PCTCROP*PINDEN	1367.4	16	2.0	0.092
FULL: IDATE + IDATE^2 + HAB + HAB*IDATE + PINDEN + DUCKDEN + DUCKDEN^2 + PCTCROP + WEDGDEN + WEDGDEN^2 + HAB*PINDEN + PCTCROP*PINDEN + HAB*PCTCROP	1382.1	31	16.7	0.000
NULL	1383.4	2	18.0	0.000

Table 2.6. Model-averaged coefficient estimates, unconditional standard errors (SE), and index of importance (coefficient of variation [CV]) for covariates predicting daily survival rate of pintail nests (n = 927) at study areas in Alberta and Saskatchewan, 1997–2009.

EFFECT	Estimate	Unconditional SE	CV
IDATE	-0.135	0.067	0.495
IDATE^2	-0.118	0.042	0.360
HAB			
FALL CROP	0.873	0.237	0.272
GRASS IDLE	0.505	0.229	0.452
GRASS GRAZED	0.220	0.171	0.776
HAY	0.443	0.195	0.439
WETLAND	-0.291	0.315	1.085
PINDEN	-0.112	0.046	0.409
DUCKDEN	-0.106	0.052	0.493
DUCKDEN^2	0.003	0.001	0.523
PCTCROP (IN PCTCROP*PINDEN MODELS)	-0.020	0.010	0.507
PCTCROP*PINDEN	0.003	0.001	0.525
HAB*IDATE			
FALL CROP	0.211	0.200	0.945
GRASS IDLE	-0.267	0.163	0.610
GRASS GRAZED	-0.083	0.149	1.802
HAY	0.293	0.170	0.581
WETLAND	0.366	0.361	0.985
WEDGDEN	-2.369	1.364	0.576
WEDGDEN^2	0.620	0.381	0.614

Table 2.7. Model suites and models examining nest habitat preference as a function of variables affecting nest survival at study areas in Alberta and Saskatchewan, 1997–2009. Best-approximating models are those within 2 Akaike Information Criterion (AIC) units of the top ranked model in each suite. Model suites differ in their inclusion of either a categorical definition of habitat type (HAB; Table 1), or habitat defined by a continuous variable (HAB_DSR) representing habitat-specific daily nest survival rate (DSR) as estimated from the nest survival analysis. Other variables identified as affecting nest survival include clutch initiation date (IDAT3CAT; categorical representing early, mid, and late initiations), pintail pair density (PINDEN), and percent grassland within study areas (PCTGRASS). No competing models to top ranked models (i.e., structurally simpler and/or containing alternate covariates than the top ranked model; Arnold 2010) are present. All models with interaction terms include main effects. The NULL model includes intercept and random effect terms for reference.

MODEL	Parameters	AIC	ΔAIC	Model weight (w_i)
HAB SUITE				
HAB*IDAT3CAT + HAB*PINDEN + HAB*PCTGRASS	31	6083.45	0	0.818
HAB*IDAT3CAT + HAB*PINDEN	25	6087.04	3.62	0.134
HAB*IDAT3CAT + HAB*PINDEN + HAB*PCTGRASS + HAB*DUCKDEN	37	6089.15	5.65	0.049
HAB*IDAT3CAT	19	6102.02	18.63	0.000
HAB	7	6123.83	40.48	0.000
HAB_DSR SUITE				
HAB_DSR*IDAT3CAT + HAB_DSR*PINDEN + HAB_DSR*PCTGRASS	11	6129.57	0.00	0.635
HAB_DSR*IDAT3CAT + HAB_DSR*PINDEN + HAB_DSR*PCTGRASS + HAB_DSR*DUCKDEN	13	6131.19	1.62	0.282
HAB_DSR*IDAT3CAT + HAB_DSR*PCTGRASS	9	6134.30	4.73	0.060
HAB_DSR*PCTGRASS	5	6136.18	6.61	0.023
HAB_DSR	3	6146.21	16.64	0.000
NULL	2	6216.96	-	-

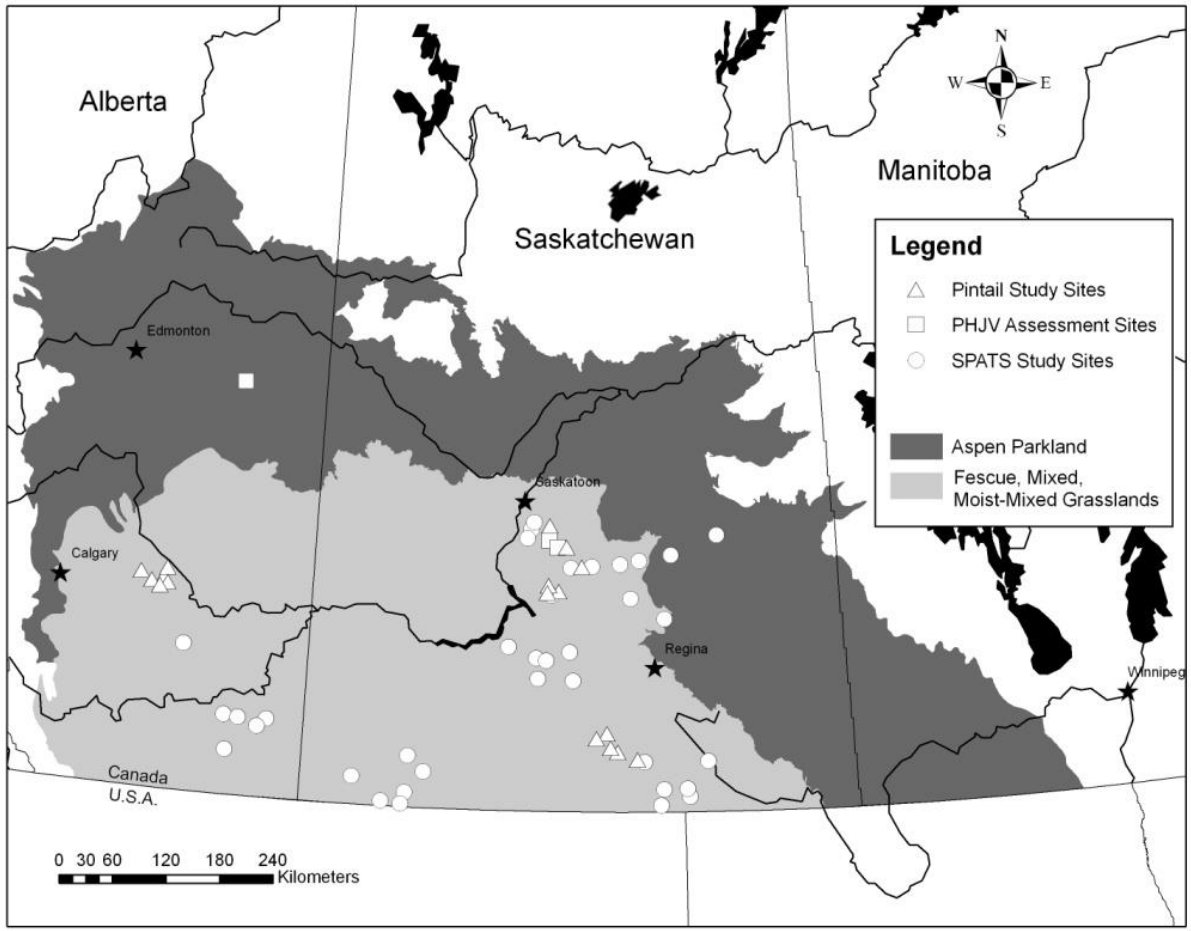

Figure 2.1. Location of Pintail, Prairie Habitat Joint Venture (PHJV) Assessment, and Spatial and Temporal Nesting Study (SPATS) sites within the Grassland and Aspen Parkland Ecozones of southern Alberta and Saskatchewan, 1997−2009.

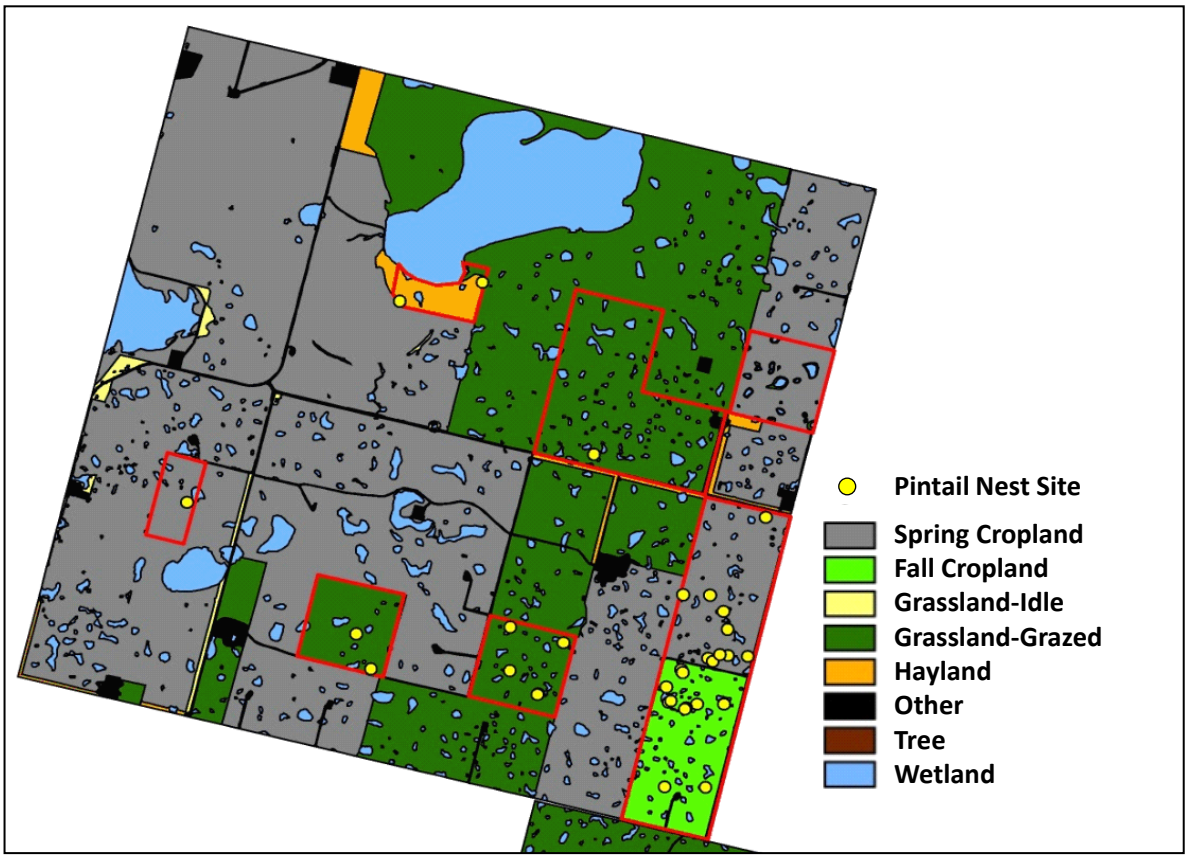

Figure 2.2. Example of digitized habitats, areas searched for ≥ 3 times waterfowl nests (outlined in red), and pintail nests located during nest searches (yellow dots) at the Hussar, Alberta (Pintail Study) study area, 2007. Few pintails nested in woodland (tree) habitat.

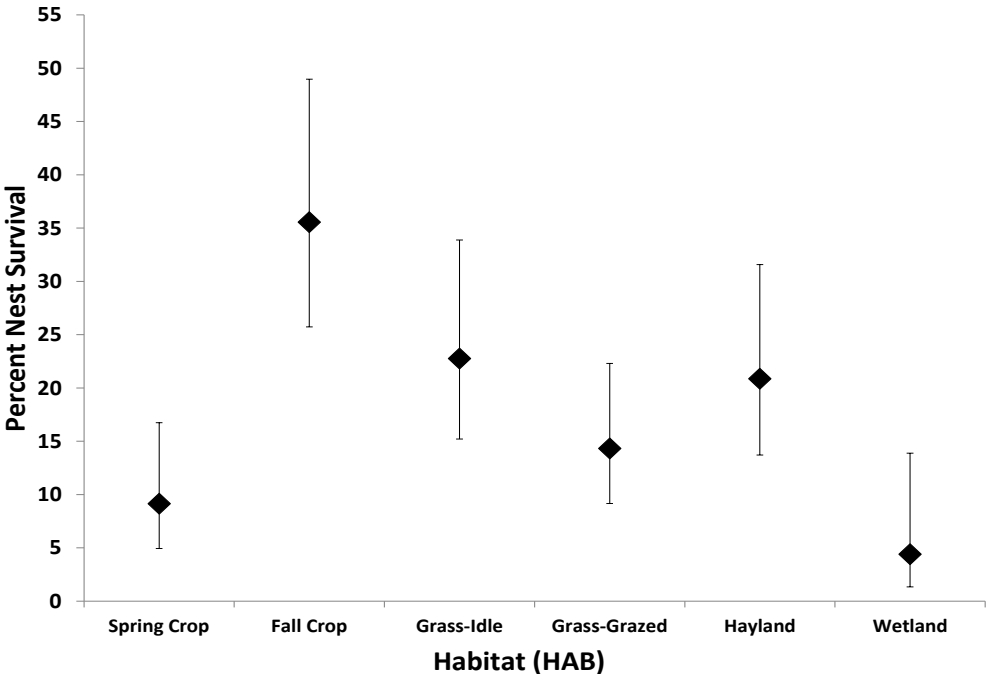

Figure 2.3. Estimated pintail nest survival (%, ± 85% CI) by habitat at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the best-approximating model (Table 2.5).

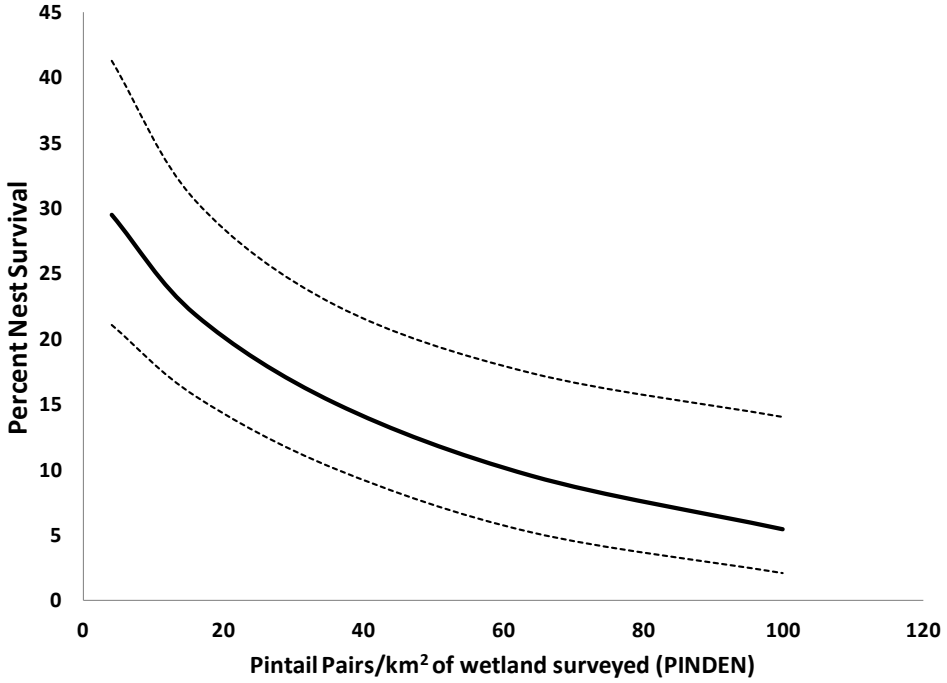

Figure 2.4. Estimated pintail nest survival (%, ± 85% CI) in relation to density of pintail pairs at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the best-approximating model (Table 2.5).

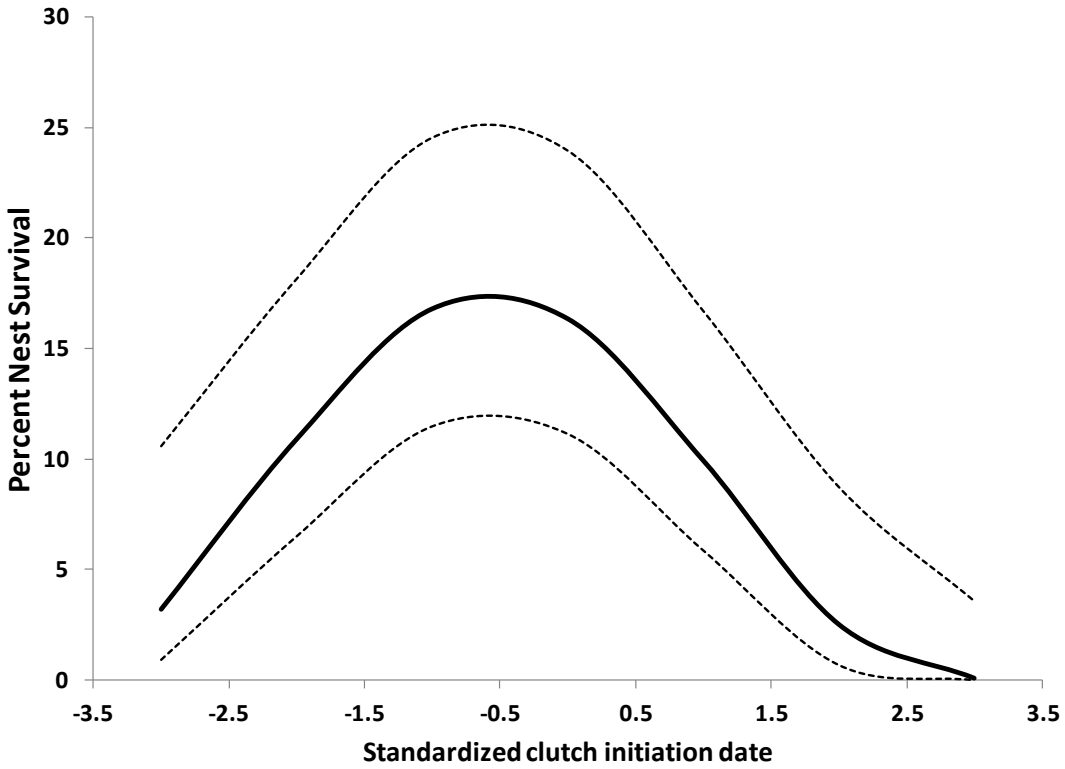

Figure 2.5. Estimated pintail nest survival (%, ± 85% CI) variation with standardized clutch initiation date at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the best-approximating model (Table 2.5).

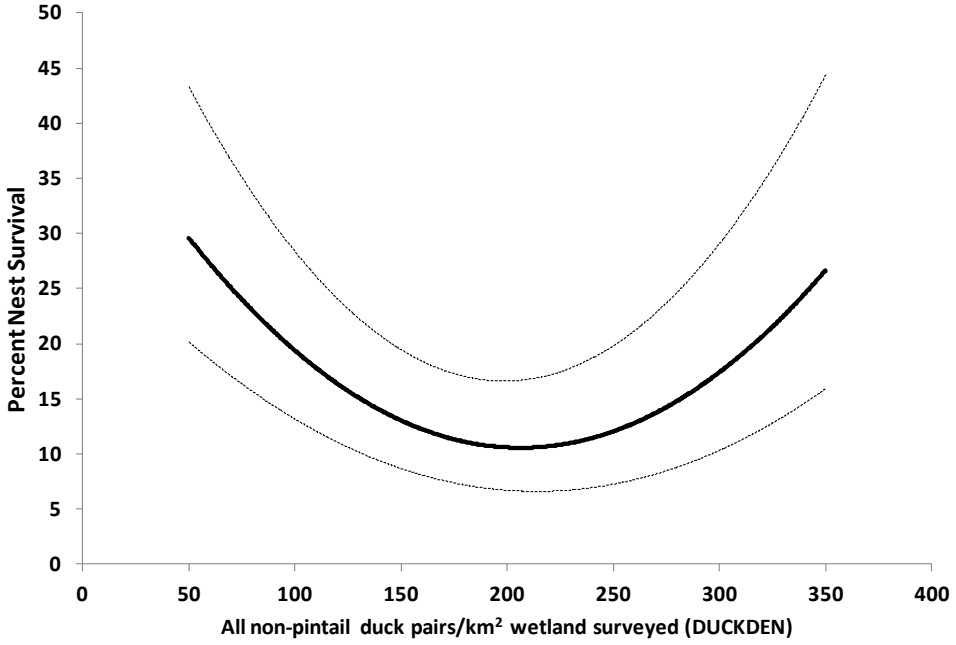

Figure 2.6. Estimated pintail nest survival (%, ± 85% CI) in relation to duck density (excluding pintails) at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the second-ranked model in Table 2.5.

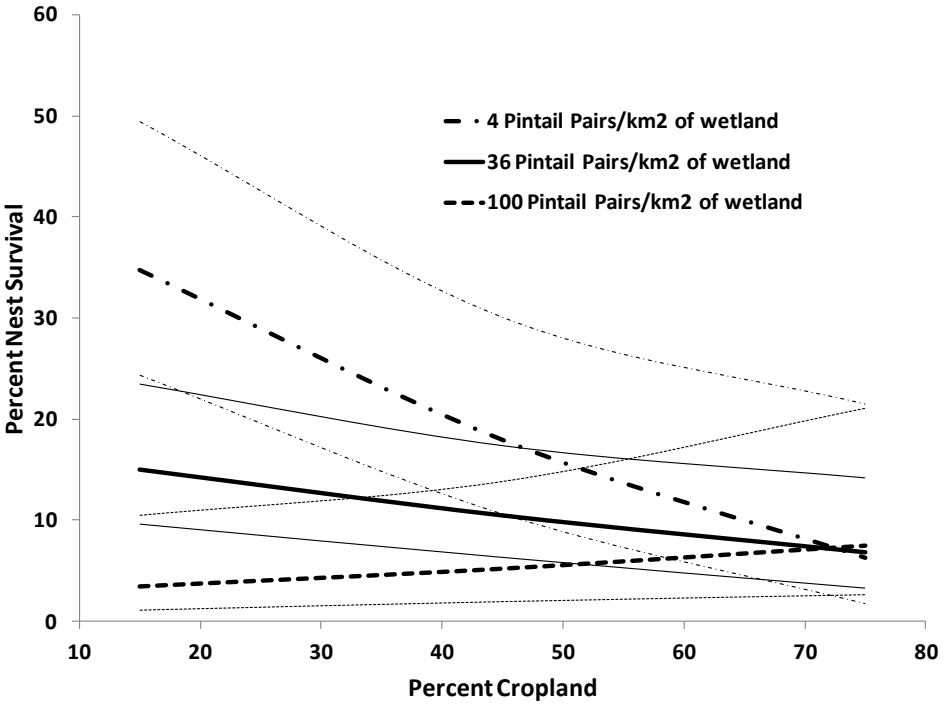

Figure 2.7. Predicted pintail nest survival (%, ± 85% CI) variation with percent cropland in the landscape at low, medium, and high pintail pair densities at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the second-ranked model in Table 2.5.

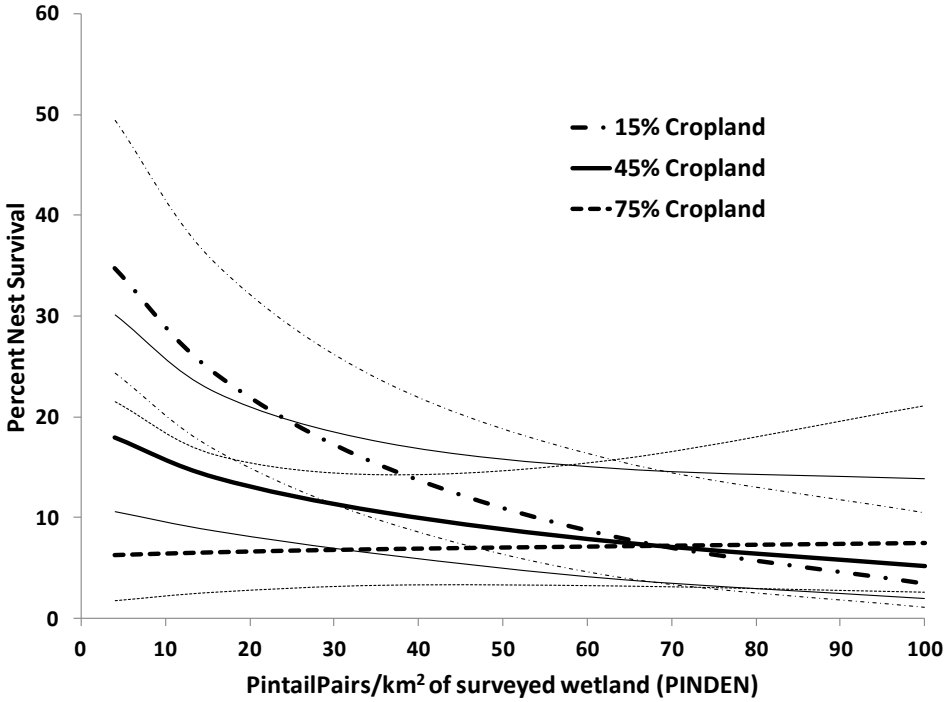

Figure 2.8. Estimated pintail nest survival (%, ± 85% CI) variation with pintail pair density at low, medium, and high percent cropland in the landscape at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived from the second-ranked model in Table 2.5.

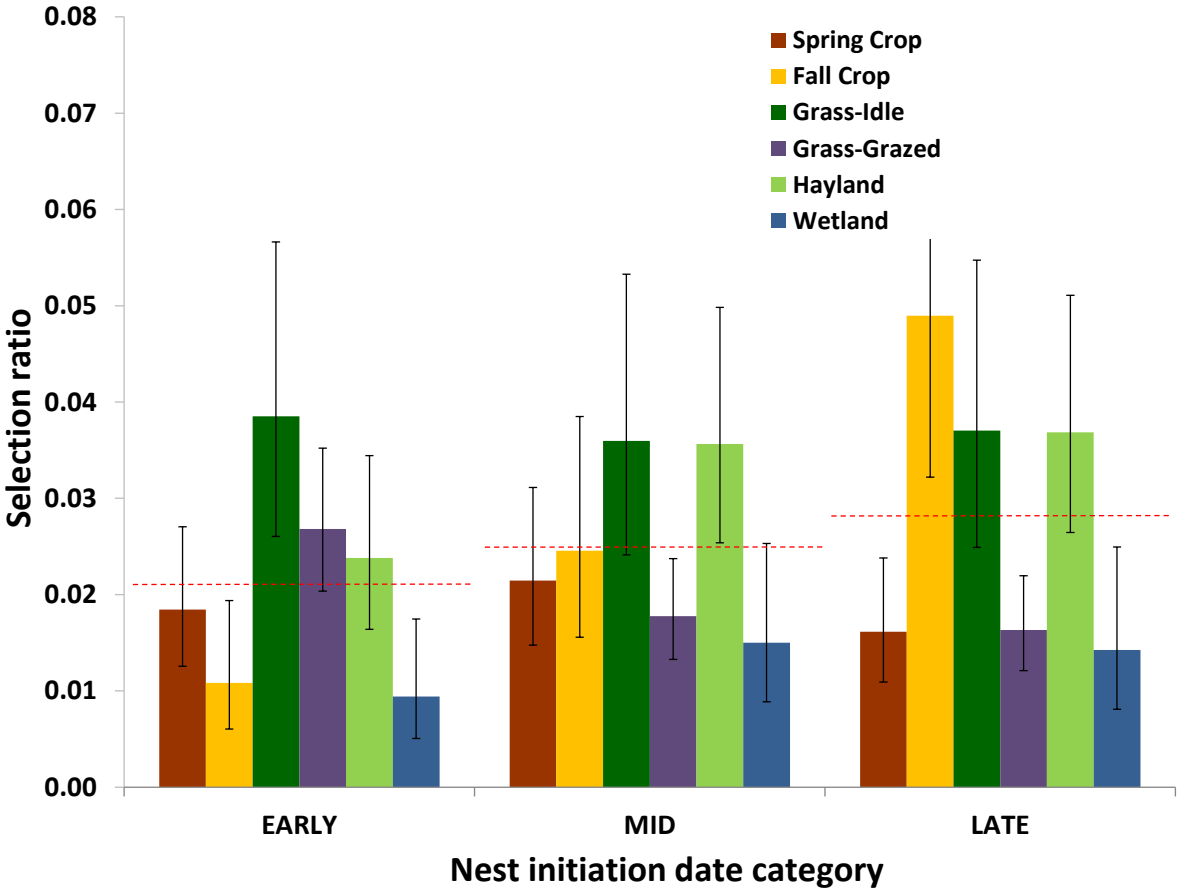

Figure 2.9. Estimated pintail nest site preference (selection ratios ± 85% CI) among habitats for early, mid and late clutch initiations at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB Suite' in Table 2.7. Dashed red lines indicate the average selection ratio within initiation date categories and represent the expected selection ratio if habitats were selected in proportion to their availability.

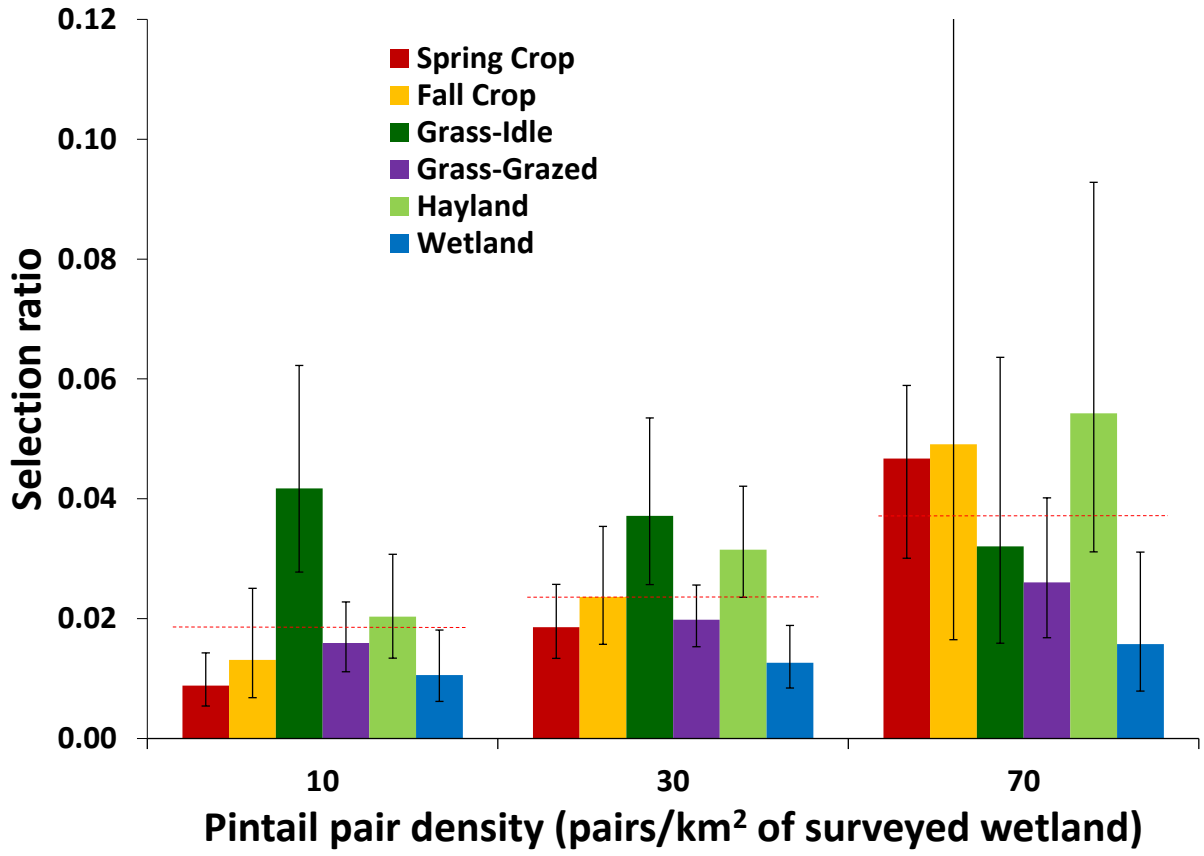

Figure 2.10. Estimated pintail nest site preference (selection ratios ± 85% CI) at low, medium, and high pintail pair density at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB Suite' in Table 2.7 applying equal weight across nest initiation date categories. Dashed red lines indicate the average selection ratio within initiation date categories and represent the expected selection ratio if habitats were selected in proportion to their availability.

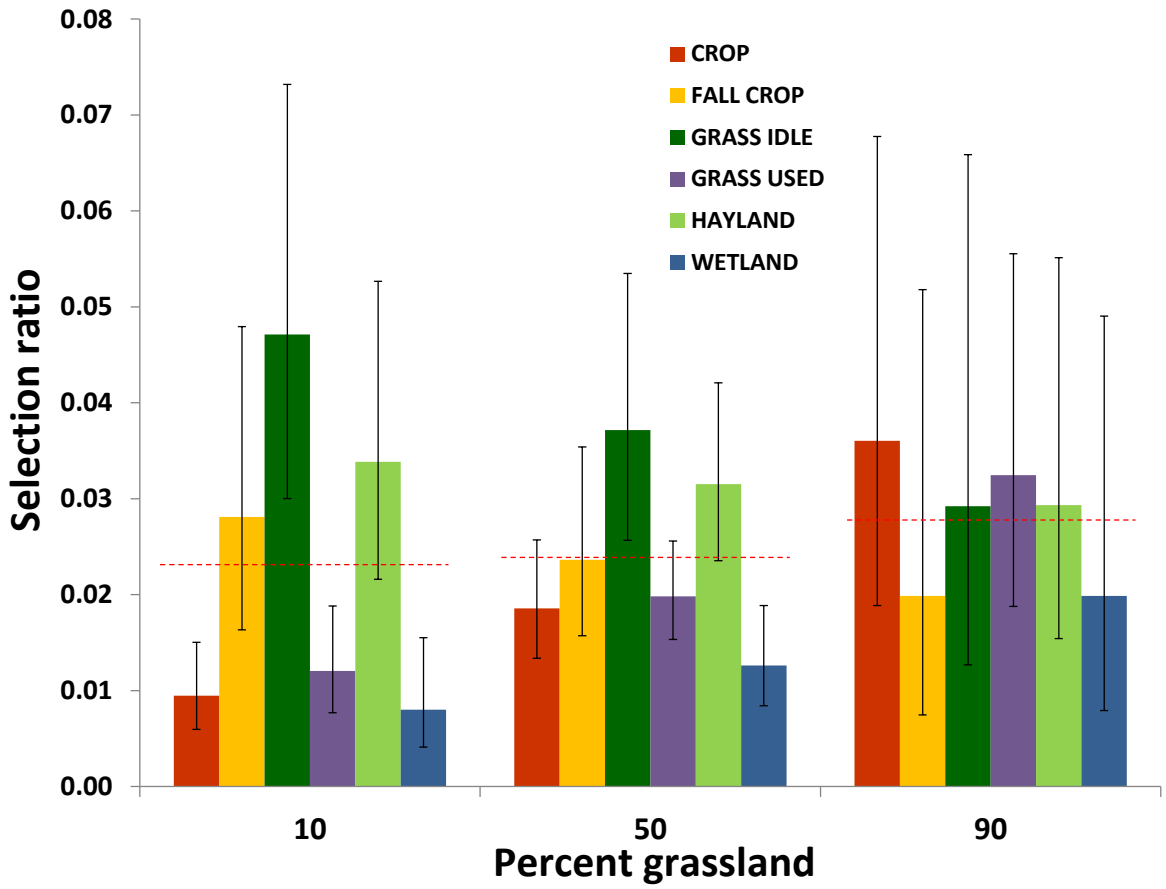

Figure 2.11. Estimated pintail nest site preference (selection ratios ± 85% CI) at low, medium, and high landscape percent grassland at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB Suite' in Table 2.7 applying equal weight across nest initiation date categories. Dashed red lines indicate the average selection ratio within initiation date categories and represent the expected selection ratio if habitats were selected in proportion to their availability.

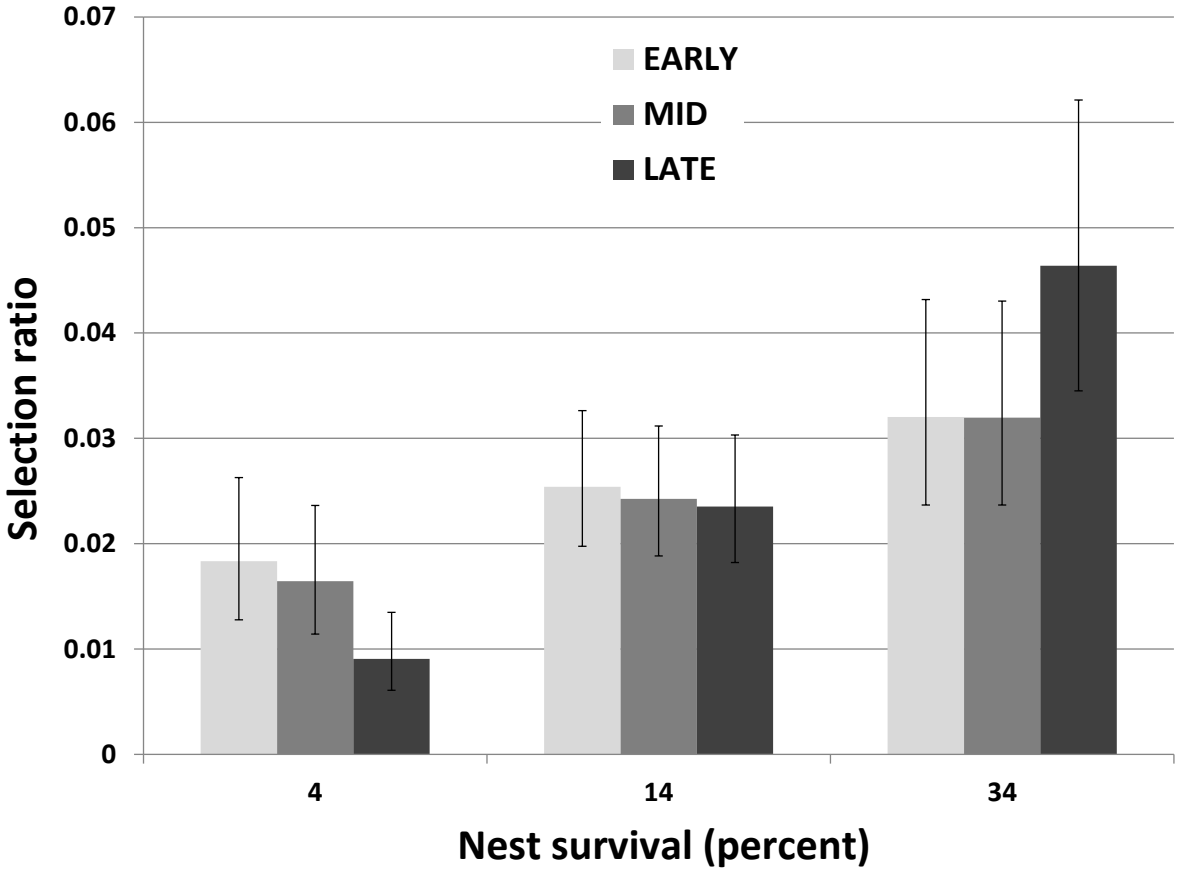

Figure 2.12. Estimated pintail nest site preference (selection ratios ± 85% CI) with pintail nest survival (%) for early, mid, and late clutch initiations at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB_DSR Suite' in Table 2.7.

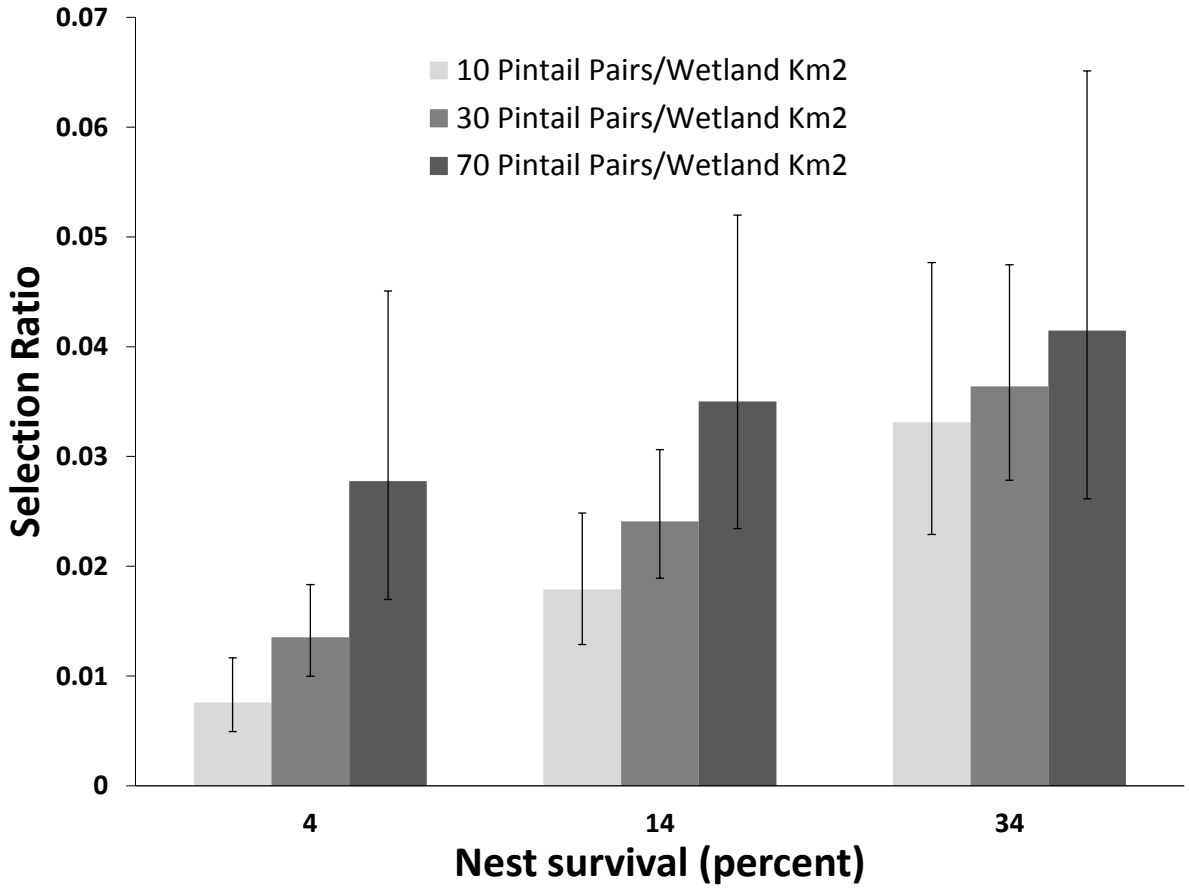

Figure 2.13. Estimated pintail nest site preference (selection ratios ± 85% CI) with pintail nest survival (%) at low, medium and high pintail density for study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB_DSR Suite' in Table 2.7 applying equal weight across nest initiation date categories.

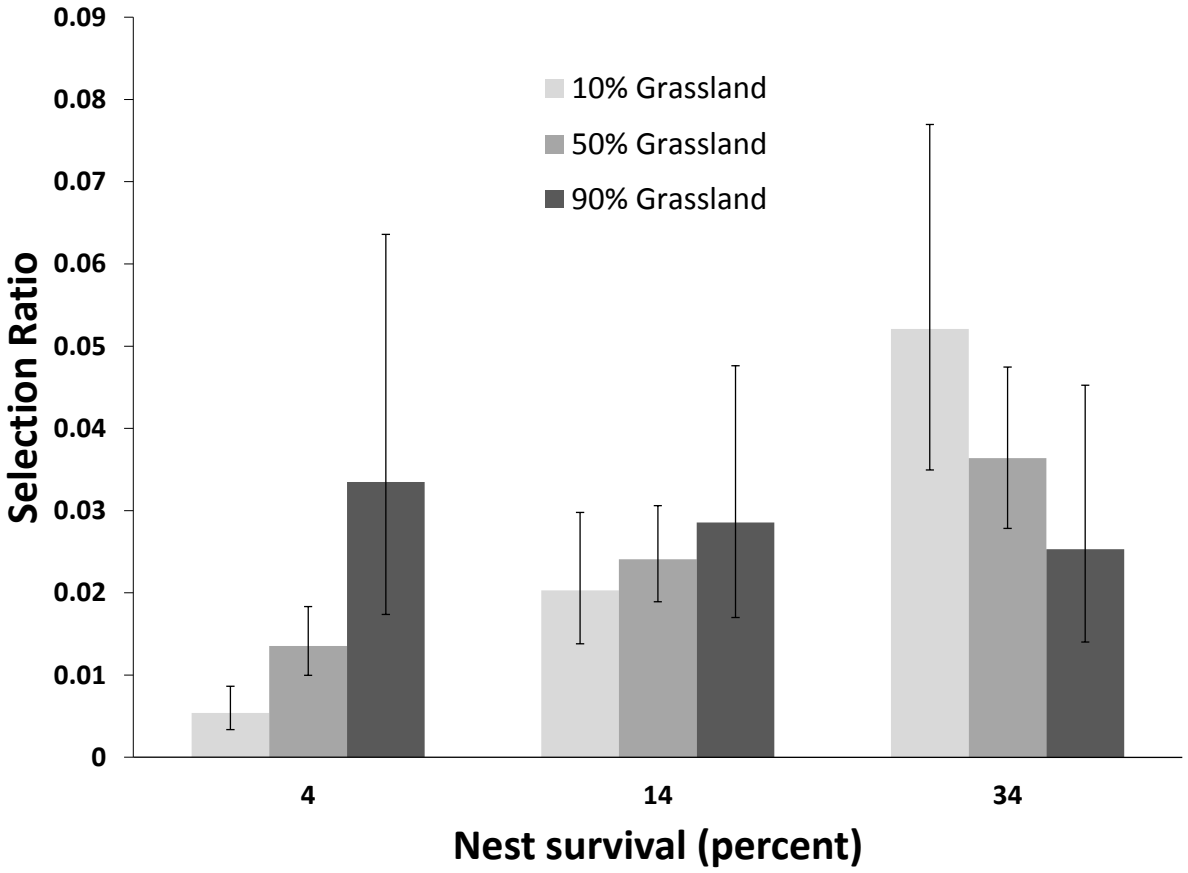

Figure 2.14. Estimated pintail nest site preference (selection ratios ± 85% CI) with pintail nest survival (%) at low, medium and high landscape percent grassland at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB_DSR Suite' in Table 2.7 applying equal weight across nest initiation date categories.

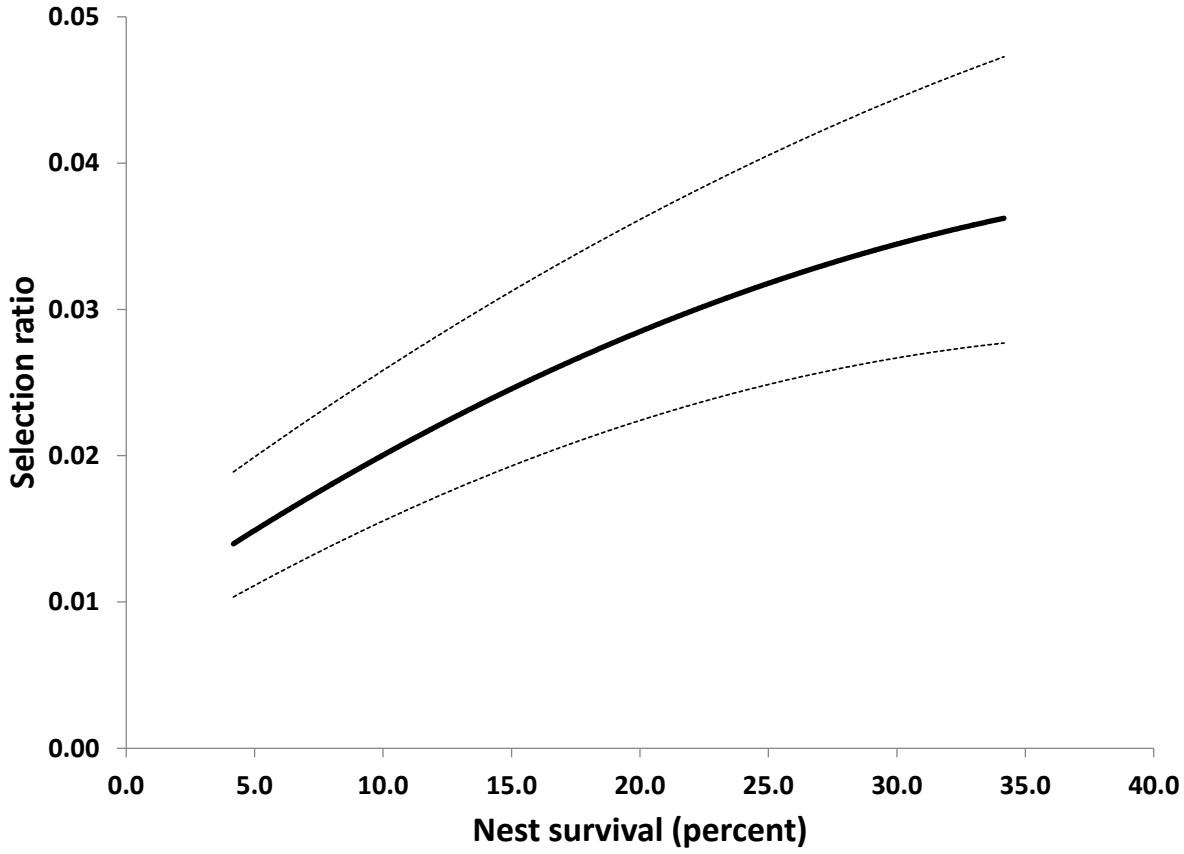

Figure 2.15. The relationship between pintail nest site preference (selection ratios ± 85% CI) and nest survival at study areas in Alberta and Saskatchewan, 1997−2009. Estimates were derived using the best-approximating model from the 'HAB_DSR Suite' (Table 2.7) using average continuous covariate values and applying equal weight across nest initiation date categories.

CHAPTER 3. LANDSCAPE ASSOCIATIONS OF NORTHERN PINTAILS IN THE PRAIRIE POTHOLE REGION OF NORTH AMERICA

3.1 Introduction

Evolutionary theory predicts that individuals exposed to gradients in fitness among habitats should select those habitats that maximize fitness or minimize the cost-benefit ratio of occupying the habitat (Fretwell and Lucas 1969, Jaenike and Holt 1991, Martin 1998, Misenhelter and Rotenberry 2000). The components of fitness for birds may depend on habitat characteristics at multiple scales ranging from nest or foraging sites to breeding or wintering ranges (e.g., Orians and Wittenberger 1991, Battin and Lawler 2006, Howerter et al. 2008). Furthermore, fitness consequences may be scale-dependent because external effects on habitat such as disturbance regimes are also scale-dependent (Opdam and Wiens 2002, Chalfoun and Martin 2007). Because *a priori* knowledge of expected fitness is generally unavailable, successful species presumably have evolved the ability to identify proximate habitat cues that reliably reflect fitness potential at the scales that are important (Misenhelter and Rotenberry 2000, Rolstad et al. 2000). Hence, in the absence of disrupting cues (e.g., Schlaepfer et al. 2002, Gilroy and Sutherland 2007), patterns of habitat use by individuals should emerge as a consequence of behaviours adapted to maximize fitness (Clark and Shutler 1999, Jones 2001, Kristan et al. 2007) and the association of population settling patterns and fitness cues is expected to be high.

For migratory birds, the annual process of migration from wintering to breeding areas presents a natural hierarchy of habitat choices in time and space as individuals decide where and when to breed. Johnson (1980) characterized this hierarchy as selection of, 1) geographic (or breeding) range; 2) home range; 3) habitat components within the home range; and finally, 4) specific resources used (e.g., food items, nest sites). While presented by Johnson (1980) as a

categorical hierarchy, habitat selection arguably occurs at a continuum of scales. For example, species exist within their geographic range at varying densities across space suggesting a level of selection between geographic and home ranges (e.g., Cunningham and Johnson 2006, Thogmartin et al. 2006; hereafter "landscape selection"). Natural variation in the quality and availability of resources at all scales creates the potential for habitat choices to produce varying fitness consequences.

In temperate breeding dabbling ducks, the ability to assess landscape cues signaling reproductive success and survival should be very highly tuned; most species nest on the ground and in the process of laying and incubating nests, suffer very high mortality rates of nests (~80-90%; e.g., Greenwood et al. 1995, Drever et al. 2004) and hens (~25%; Devries et al. 2003). While upland-nesting ducks are adapted to high mortality rates (i.e., high reproductive capacity; nest as yearlings, large clutch sizes, multiple renests), several species, especially the northern pintail (*Anas acuta*), have undergone population declines that have sparked much interest in understanding the role of habitat selection as a mechanism in their decline (e.g., Miller and Duncan 1999, Podruzny et al. 2002). As of 2012, pintail populations in the southern survey strata of prairie Canada were 50% below long-term average. In contrast, all other prairie nesting dabblers ranged from 13% to 110% above long-term averages (Zimpher et al. 2012). Modeling efforts have suggested that factors associated with reproductive success, especially in the Prairie Pothole Region, are likely limiting pintail population recovery (Hestbeck 1996, Miller and Duncan 1999, Shaeffer et al. 1999, Mattsson et al. 2012). While work has focused on factors associated with individual reproductive success (e.g., Guyn and Clark 1999), little effort has been directed at factors limiting reproductive success at larger scales.

At landscape scales (e.g., scales of 5–50 km^2), both wetland and upland habitat cues may be used in settling decisions (Krapu et al. 1997, Austin et al. 2001, Mack and Clark 2006) and these are likely readily assessed by breeding pintails (e.g., Hutto 1985, Podruzny et al. 2002). Pintails are unique among North American dabbling ducks in their nomadic wanderings in response to annual wetland conditions and their propensity to settle in "open country" with low vegetation and shallow, intermittently flooded wetlands (Johnson and Grier 1988, Austin and Miller 1995). More than other dabbling ducks, pintails are strongly associated with shallow tilled wetlands in highly cultivated landscapes, especially in wet years (Stewart and Kantrud 1973, Krapu 1974). Association with highly cultivated landscapes may expose pintails to lower nest survival given their propensity to nest in croplands where nest loss is high (Miller and Duncan 1999, Richkus 2002). However, population-level demographic consequences of these general habitat associations remain poorly quantified.

How pintails associate with landscapes at multiple scales, and resulting demographic consequences, is of considerable practical and theoretical interest. The objective of this study, therefore, is to examine whether pintail distribution and reproductive success within the PPR relative to key landscape characteristics are linked in ways consistent with evolutionary theory. Specifically, I examine whether annual population-level indices of recruitment (i.e., higher juvenile:adult age ratios of autumn harvested birds) are associated with pintail distribution relative to geographic and landscape characteristics the preceding breeding season – patterns that should reflect probability of reproductive success if breeding pintails adaptively select breeding landscapes. I then determine whether pintail counts on long-term breeding population survey transects reflect patterns of association with landscape variables linked to measurements of local

and population-level recruitment. In both analyses, I consider the effects of regional population size and test for evidence of density-dependence in landscape association-fitness relationships.

3.2 Hypotheses and Predictions

I use large observational datasets of pintail counts and annual harvest rates to examine associations with spatially and temporally varying landscape covariates from within the PPR. My inferences about adaptive habitat associations, therefore, are based on correspondence between evidence of an annual reproductive effect at the population level, and population-level habitat associations observed during the preceding breeding season. My choice of habitat variables that define associations is tempered by evidence of potential impacts on components of reproductive success suggested in existing literature.

Like most waterfowl, pintails are highly adapted to wetland habitat for most aspects of their life cycle, such as resting cover and food resources (especially during egg formation and brood rearing; Austin and Miller 1995). In the PPR, breeding pair densities are positively correlated with wetland area and number of seasonal and semi-permanent wetlands (Stewart and Kantrud 1974) and pairs are typically most numerous on small, shallow seasonal wetlands (Stewart and Kantrud 1973). Wetland area and number, therefore, are expected to have a positive relationship with pintail numbers and these relationships are generally expected to be nonlinear (e.g., Cowardin et al. 1995, Bartzen 2008). There may be trade-offs for pintails nesting in wetland-dense landscapes, however, as predators recognize wetland edges as profitable foraging sites (e.g., Larivière and Messier 2000, Phillips et al. 2003), potentially resulting in higher nest predation (e.g., Howerter 2003, Stephens et al. 2005). However, higher nest predation may be offset by higher duckling survival in wetland-rich landscapes (Rotella and Ratti 1992).

Because the PPR is prone to periodic drought-deluge conditions, and given the pintail's predilection for seasonal wetlands, annual moisture regime is expected to further modify decisions regarding landscape selection (e.g., Smith 1970, Henny 1973, Derksen and Eldridge 1980, Johnson and Grier 1988). I predict that indices of local wetness linked to winter precipitation immediately prior to the breeding season, and carry-over of water from previous years, will have a positive influence on pintail counts (e.g., Stewart and Kantrud 1974, Johnson and Grier 1988, Cowardin et al. 1995, Bartzen 2008). Numerous studies have documented higher reproductive success of waterfowl (both locally and at the population level) in years with abundant spring moisture (e.g., Cowardin et al. 1985, Kaminski and Gluesing 1987, Greenwood et al. 1995) so I predict recruitment indices will reflect landscape selection relative to annual wetness indices within the PPR. Because relationships between pintails and wetlands and annual moisture regimes have been relatively well documented, especially in the PPR, these components comprise a baseline biological null model to which additional covariates may be added to represent alternate hypotheses about pintail landscape associations.

I predict the size of the PPR breeding pintail population will affect several aspects of pintail recruitment and habitat association through density-dependent mechanisms. At the breeding range scale, Runge and Boomer (2005) demonstrated negative density-dependence in recruitment at the population level, modified by annual wetness regimes in the Canadian prairies. Generally, when the prairies are wet and more pintails settle in this region, recruitment increases. Thus, I expect population-level recruitment to increase as pintail population in the PPR increases. It also is possible that pintail density will mediate habitat associations in the PPR. In general, I expect a greater use of marginal quality landscapes when populations are high if superior quality individuals exclude or displace lower quality individuals into less suitable

landscapes (Brown 1969, Rodenhouse et al. 1997). To further examine putative density-dependent effects on recruitment, I include PPR population size as an interacting covariate in my analyses.

Several studies have documented land-use effects at the landscape scale affecting waterfowl recruitment; generally, nest survival tends to be lower in cropland-dominated landscapes and higher in grassland-dominated landscapes (Greenwood et al. 1995, Horn et al. 2005, Stephens et al. 2005). Because most waterfowl tend to avoid cropland as nesting habitat, reduction in available nest habitat in cropland-dominated landscapes is thought to concentrate nests into remaining habitats (road ditches, fencerows, wetland margins) that are easily, and more profitably, searched by predators (Sovada et al. 2000, Phillips et al. 2003, Horn et al. 2005). Unlike most other duck species, pintails readily nest in cropland stubble where nests are frequently destroyed by predators or spring tillage operations (e.g., Milonsky 1958, Klett et al. 1988, Richkus 2002, Devries et al. 2008a). These characteristics would suggest that when pintail settlement within the PPR is weighted toward cropland- or grassland-dominated landscapes, the recruitment signal in the fall harvest should be lower or higher, respectively. If so, adaptive landscape association would predict that pintails should avoid cropland-dominated landscapes and demonstrate a strong affinity for grassland-dominated landscapes. Alternatively, if pintails tend to associate with cropland-dominated landscapes, this may represent an ecological or evolutionary trap as some authors have speculated (Miller and Duncan 1999, Richkus 2002). If the association with cropland occurs only at high pintail density, a buffer or site-dependent effect will be supported.

Pintails are described as frequenting relatively flat to gently rolling grasslands and are known for opportunistic use of the shallow temporary and seasonal wetlands that characterize

these landscapes (Stewart and Kantrud 1973, Johnson and Grier 1988, Austin and Miller 1995). Shallow, temporary and seasonal wetlands are typically the first wetlands available in spring due to rapid spring thaw and they typically are rich in invertebrate foods required by breeding females (Krapu 1974). These wetlands also are subject to more rapid and frequent water loss by evapo-transpiration resulting in greater temporal variability (Nudds 1983, Euliss et al. 2004), producing greater variation in waterfowl productivity (e.g., Herfindal et al. 2012, Walker et al. 2013). The variable nature of these landscapes also may reduce their ability to support stable predator populations (e.g., Sargeant et al. 1984, Krapu et al. 2004, Walker et al. 2013). Because no database exists for prairie Canada that separates wetlands by class, I use landform as a proxy for wetland type; flatter landscapes are assumed to have more seasonal wetlands and more rolling landscapes presumably have more semi-permanent/permanent wetlands. Hence, after accounting for effects of wetland area and abundance, I predict that pintails will exhibit higher recruitment when they are associated with flatter landscapes. If pintails associate with more rolling landscapes only at high population level, a buffer or site-dependent effect will be indicated.

Geographic patterns in pintail settling patterns within the PPR have been described by several authors (e.g., Johnson and Grier 1988, Podruzny et al. 2002). Years of survey data indicate that pintail abundance has tended to be greater in western and southern regions of the PPR and that, depending on wetland conditions, pintails may settle opportunistically from south to north during spring migration (i.e., in March-April; Johnson and Grier 1988). In addition, pintails are known for breeding in "open country" with "low upland cover" more typical of the Grassland biome versus the more northern Parkland biome of the PPR (Austin and Miller 1995). Emerging geographic patterns in nest survival in the PPR (i.e., higher to the west and south;

Reynolds et al. 2001, DUC unpublished data) suggest adaptive value in this distribution. Additional benefits may accrue from earlier breeding opportunities and reduced migration costs (Daan et al. 1989, Kokko 1999, Krapu et al. 2000). I therefore predict that pintails will show a greater association with southern and western locations within the PPR and that population-level recruitment indices will be higher in years when populations are distributed further south and west in the PPR. If geographic association shows evidence of northward or eastward shifts at higher PPR populations, buffer or site-dependent effects will be suggested.

3.3 Study Area and Methods

3.3.1 Study Area and Scope

I used several spatial and temporal datasets to examine relationships between pintail distribution within the PPR, continental population-level recruitment indices, and local PPR habitat covariates. I limited my investigation to the PPR because this region is the primary breeding region for pintails in the midcontinent of North America, and detailed spatial datasets are more readily available for this region. Here, I defined 'landscapes' as areas as small as the area surveyed within transect segments (~13 km^2) but including up to the size of study sites used in Ch. 4 (41 km^2) and elsewhere (e.g., Stephens et al. 2005). I limited investigation to the time period 1961–2009 because visibility-corrected pintail abundance estimates (see below) were available only from 1961 onward (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987).

3.3.2 Pintail recruitment estimates

First, I examined whether the distributions of pintails within the PPR relative to landscape characteristics 'signal' a response in annual population-level indices of recruitment. I used the

vulnerability-corrected juvenile:adult ratio of female pintails harvested annually in the U.S. harvest for the period 1962-2003 (Runge and Boomer 2005) as an index to annual recruitment. Vulnerability-corrected age ratios adjust raw age ratios in the hunter bag for differential vulnerability of age and sex classes to hunting (Geissler 1990). Female age ratios are determined from wings of hunter-killed birds collected from across the United States and Canada as part of the annual Parts Collection Survey (Couling et al. 1982, Geissler 1990).

3.3.3 Pintail and pond counts

I used pintail and pond count data collected as part of the Waterfowl Breeding Population and Habitat Survey conducted annually in May (WBPHS; U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). I used counts collected during 1961–2009 along 809 systematically located permanent survey transect segments located within 23 survey strata (strata 26–35, 37–41, and 45–49) spanning the PPR of Canada and the U.S. (Figure 3.1). Survey transects are systematically spaced within strata and each transect consisted of 2–11 survey segments, each ~29 km in length and 0.4 km in width (11.6 km^2 in area) to which counts are coded. Procedures for conducting surveys and evaluations of their efficacy were described in detail by Bowden (1973) and Benning (1976).

Survey biologists record the numbers of all pintails and ponds seen from a fixed-wing aircraft flying ~160 km/h at 30–46 m AGL along survey transects. Species are counted as pairs (male and female in close association), lone males, grouped males <5, and groups (mixed-sex groupings in close association, and ≥ 5males in a group). Class III–V wetlands (seasonal-permanent 'ponds'; Shaw and Fredine 1956), streams and rivers crossing transects, and artificial wetlands (dugouts, stock dams etc.) containing water are counted as an annual index to availability of habitat (Turner et al. 1987). Concurrent with aerial waterfowl and pond counts,

biologists conduct complete ground surveys on a sub-sample of survey segments (~50) to establish visibility-correction factors which are applied to aerial counts at the stratum level (hereafter, visibility-corrected counts). Survey segment level count data used in this analysis were downloaded from the USFWS Office of Migratory Bird Management online data portal (https://migbirdapps.fws.gov/). The survey segment was the experimental unit in my analyses. I used indicated breeding pintail pairs (i.e., visibility-corrected observed pairs + lone males + grouped males <5; Dzubin 1969a, Hammond 1969) as the response variable in my analysis of landscape-level habitat associations.

3.3.4 Spatial and temporal covariates

I selected spatial and temporal variables that were available across the PPR because my intent was to understand factors associated with the distribution of breeding pintails across the entire region, and also to extrapolate model estimates to the spatial extents of the PPR (see Ch. 4). Covariates were generally extracted within, or associated with, the boundary of the surveyed area of each survey segment in ArcGIS.

Because ducks are wetland obligate species, I included the best available data for the spatial distribution of wetland numbers (count) and area (ha) for the PPR. In Canada, wetland count and area were derived from digital hydrography and saturated soils features in the CanVec database (Edition 1.2.2; Natural Resources Canada 2011). Because CanVec hydrography fails to detect small wetland basins, I used overlapping CanVec and Ducks Unlimited Canada high-resolution wetland inventories for 1,371 – 41.4 km^2 grid blocks, and constructed separate wetland area and count adjustment models (i.e., DUC Inventory/CanVec; DUC unpublished data). Adjustment models included the effects of province, soil landscape variables (Canadian Soil Information System 2011; drainage, surface form, water holding capacity), and number and area of small

CanVec basins (i.e., small = <0.5 ha; rationale: more basins are missed where there are many small wetland basins). The best-approximating adjustment models were then applied in ArcGIS to covariates extracted from a set of 41.4 km^2 grid blocks covering prairie Canada. An adjusted wetland area and count surface was then created by multiplying raw CanVec wetland area and count by spatially coincident adjustment factors. Finally, estimated wetland area and count were extracted as the focal mean of pixel values within survey segment boundaries.

Within the U.S. PPR, wetland area and count were extracted along survey segments from the National Wetlands Inventory database (NWI; U.S. Fish and Wildlife Service 2011). No adjustments were made as NWI is a high-resolution wetland-specific database. Wetland area (WETHA) and wetland count (WETCNT) from both Canadian and U.S. datasets were transformed to normality with natural log and square root transformations, respectively.

Annual moisture regimes, affecting the availability and condition of wetlands in the spring, affect breeding season settlement by ducks (e.g., Johnson and Grier 1988, Austin and Miller 1995). Hence, I examined 2 sources of information to determine annual and spatial variation in spring wetland conditions. First, I standardized segment and year-specific WBPHS pond counts (Benning 1976) relative to their long-term (1961–2011) median values using Median Absolute Deviations in PROC STDIZE in SAS (SAS Institute, Inc., Cary, NC). This created an annual index (PONDINDEX) with relatively greater negative to positive values representing locally drier and wetter conditions, respectively. As an alternative, I used global 2.5° gridded monthly Palmer Drought Severity Index (PDSI) data for May (self-calibrated with the Penman-Monteith potential evapotranspiration formulation, 1900–2010; Dai 2011) downloaded from the National Center for Atmospheric Research (Boulder, CO, USA; http://www.cgd.ucar.edu/cas/catalog/climind/ pdsi.html). I interpolated gridded values across

the PPR in ArcGIS using inverse distance weighting, and then estimated segment-specific PDSI values using focal mean pixel values within survey segment boundaries. Because wet years can have long-lasting effects, I included one year lags for both PONDINDEX (LAGPOND) and PDSI (LAGPDSI). Annual wetness indices were square root transformed to improve normality.

I estimated two alternate land cover metrics to characterize the degree of agricultural intensity associated within survey segments; percent annual cropland (PCTCROP), and percent grassland (PCTGRASS). PCTCROP and PCTGRASS were estimated from digital land cover products produced by Agriculture and Agri-Food Canada (2008) and the U. S. Geological Survey (Homer et al. 2007) representing land cover circa 2000 and 2001, respectively. In Canada, PCTCROP was defined as the proportion of the survey segment in the "Annual Cropland" category, and PCTGRASS was defined as the combined proportion of "Grassland, Native Grass", and "Perennial Crops, Pasture" categories. In the U. S., PCTCROP was defined as the proportion of the survey segment in "Cultivated Crops", and PCTGRASS was defined as the combined proportions of "Grassland/Herbaceous" and "Pasture Hay". Segment level proportions were extracted using Spatial Analyst Zonal Statistics in ArcGIS.

Because pintails are generally recognized as being more prone to occupy flat to gently rolling topography than other ducks (Austin and Miller 1995) I examined two alternate measures of landform using Shuttle Radar Topography Mission (SRTM3 Version 2; 3 arc-second resolution [~90 m], edited; Farr et al. 2007) digital elevation model (DEM) data. SRTM data represent the only DEM available for the entire PPR. First, I converted the SRTM elevation grid to slope estimates using Spatial Analyst in ArcGIS. Second, I estimated the coefficient of variation in elevations within a 41 km^2 neighbourhood using focal mean and focal standard deviation statistics generated with Spatial Analyst in ArcGIS. Hence, the focal mean values of

90 m pixels for slope (MEANSLOPE) and coefficient of variation in elevation (CVSRTM) were estimated within survey segment buffers using Spatial Analyst. MEANSLOPE and CVSRTM were natural log transformed to improve normality. A small constant (0.01) was added to MEANSLOPE to facilitate transformation.

I included latitude (LAT) and longitude (LONG) to account for previously described geographic trends in pintail counts. LAT and LONG were defined by the location of the centroid of each survey segment. I divided LAT and LONG by 10 to facilitate optimization in analytical procedures.

3.3.5 Analysis of Recruitment Data

I first examined whether the distribution of pintails within the PPR relative to several geographic and landscape variables correlated with a response in the annual measurement of population recruitment gathered by the USFWS from hunter-killed birds. I used annual recruitment indices for 42 years (1962–2003) as the response variable and annual population-weighted covariates for annual wetness (WGTPOND, WGTPDSI), landscape composition (WGTCROP, WGTGRASS), landform (WGTSLOPE, WGTCVSRTM), and geographic location (WGTLAT, WGTLONG, and their first principal component; GEO_PC1) as explanatory variables. Population-weighted covariates were the sum of segment-level covariate values multiplied by the proportion of the annual PPR pintail population occurring on each survey segment. Because recruitment is known to respond to the size of the pintail population settling in the PPR, I included the size of the annual PPR breeding population in all models. I defined the annual breeding population (PPRPOP) as an index equal to the sum of within-year pintail counts across all survey segments divided by the number of segments surveyed.

I began with a global model containing PPRPOP and each covariate with their quadratic forms and an interaction between PPRPOP and the linear form of the covariate (Table 3.1). Multiple covariate models were not considered given the relatively small number of years in the sample. I used Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) relative to the null model AIC_c (using PROC GENMOD in SAS) to determine variables with evidence of an effect on pintail recruitment.

3.3.6 Analysis of Landscape Association Data

I used 37,377 pintail pair and pond counts made on 809 survey segments with complete covariate data over 48 years. I employed a two-step modeling approach to efficiently consider all covariates of interest. First, I considered two competing default, or 'biological null', models incorporating effects of biological, physical, and methodological factors expected to affect pintail counts. I included the effects of WETCNT and WETHA together in combination with an annual moisture index, either PDSI or PONDINDEX, in competing models. Further, I included each annual moisture metric lagged one year (PDSILAG1, PONDINDEXLAG1) to account for potential lagged wetness effects. Both models included quadratic effects on all covariates and first-order interactions between each wetland and annual moisture index. Because WETCNT and WETHA were taken from different sources in Canada and the USA, I included COUNTRY (USA/Canada) as a categorical variable interacting with each wetland variable to account for potential differences in response due to covariate resolution. Because counts are expected to be higher in years when more pintails settle in the PPR, I included the pintail population size index (PPRPOP) as an offset variable. I further included first order interactions between PPRPOP and WETHA and WETCNT because it is plausible that use of wetland habitat is density-dependent.

To account for variation in survey segment length, I included survey segment buffer area (SEGAREA) as an offset variable.

Zero counts comprised approximately 25% of the data so I explored various zero-inflated approaches to model evaluation. First, I examined base model fit of four zero-inflated model alternatives: zero-inflated Poisson, zero-inflated negative binomial, and the 'hurdle' model formulations of each. I used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to assess model fit among the alternatives. Best fit to the data was obtained with the zero-inflated negative binomial hurdle model, so this formulation was used for all subsequent model examination. Hurdle models are appropriate when count data contain an excess of zeros arising from 2 separate processes (Hu et al. 2011).

Zero-inflated negative binomial (ZINB) hurdle models were fitted by defining separate general likelihood functions for the binomial probability of a zero count (hereafter 'zero-count probability model') and the truncated-at-zero negative binomial count model (hereafter 'non-zero count model'). Models were fitted using PROC NLMIXED in SAS. The negative binomial model explicitly estimates a dispersion parameter to accommodate unaccounted spatial covariance and other possible sources of overdispersion (White and Bennetts 1996). Because counts resulted from annual surveys on the same segments (temporal autocorrelation), I included residual time-dependence in model structure by including a normally distributed correlated random effect in both likelihood functions.

I used a backward elimination procedure to sequentially simplify the best-approximating of the two wetland-moisture biological null model alternatives. At each step, the least-predictive covariate (i.e., the smallest F-ratio) was removed from the model. Interaction terms and

quadratics were always removed before associated main effects. The model with the lowest AIC was identified as the best-approximating wetland-moisture model.

Then, to the best wetland-moisture model, I added covariates examining land-use (PCTCROP and PCTGRASS separately), landform (MEANSLOPE and CVSRTM separately), and geographic influences (LAT and LONG together) in three model suites. Where alternate covariates were an option (e.g., PCTCROP vs. PCTGRASS), only the best-approximating model of the two was taken forward for covariate reduction and model selection. I included first order interactions with PPRPOP to examine density-dependent responses to these covariates. Again, a backward elimination procedure removing the least predictive covariate was applied (on the basis of AIC) and the best-approximating model for each covariate was identified. I included the quadratic form of geographic, land use and landform covariates retained in best-approximating models as an exploratory exercise to evaluate whether nonlinear responses provided a better fit to the data.

I present all models ranked by AIC, and consider only structurally simpler models as competitors for drawing inference (Burnham and Anderson 2002, Arnold 2010). I considered models within 2 AIC units of the best-ranked models (i.e., $\Delta AIC \leq 2$) for drawing inference (Burnham and Anderson 2002). Further, I used ΔAIC to select among competing models that contain alternate covariates. I used AIC weight (w_i) as a measure of supporting evidence for each model. I assessed the relative importance of individual covariates by examining the coefficients of variation of the parameter estimates (Arnold 2010). I report means ± 1 SE, and model effect estimates with 85% confidence limits to be consistent with information-theoretic approaches (Burnham and Anderson 2002, Arnold 2010).

3.4 Results

3.4.1 Recruitment

I examined 33 models relating annual population-level recruitment indices to pintail population size and distribution within the PPR (Table 3.1). The nonlinear form of the PPRPOP-only model provided the best fit (Table 3.1) and hence this form was taken forward in combination with each of the population-weighted landscape covariate models. This model demonstrated a positive relationship between the recruitment index and the pintail population counted within the PPR (Figure 3.2a).

Inclusion of population distribution within the PPR relative to several landscape characteristics provided improved fit to the data. Both population-weighted temporal moisture covariates (WGTPDSI and WGTPOND) demonstrated predicted positive effects (Figures 3.2 a,b). The best-approximating model for WGTPOND included the nonlinear effect and an interaction with PPRPOP (Table 3.2). The nature of the interaction indicated that recruitment had an asymptotic positive relationship with the distribution of pintails relative to pond counts when populations were high, but not when populations were low (Figure 3.2b). The best-approximating model for WGTPDSI included only the linear form of the covariate (Table 3.2) such that recruitment was highest when pintail populations were associated with locations with high PDSI values (Figure 3.2c).

The best-approximating landuse model included a marginal linear effect of WGTGRASS (Table 3.2), with no evidence of nonlinearity. This effect suggests higher recruitment indices occur when pintails are more closely associated with grassland-dominated landscapes (Figure 3.2d).

The best-approximating landform models included a marginal positive linear effect of WGTSLOPE and a strong nonlinear effect of WGTCVSRTM (Table 3.2). Recruitment indices were higher when pintails settled in landscapes with higher mean slope and in landscapes with moderately variable terrain (Figures 3.2e,f). This analysis provided no evidence that pintail distribution within the PPR relative to PCTCROP, LAT, LONG, or GEO_PC1 had discernable effects on the population recruitment index.

3.4.2 Landscape associations

I examined 28 models relating pintail pair counts to potential covariates of interest: six models to identify the best wetland-moisture covariates, five models to identify the best land use effects, six models to identify the best landform associations, seven models to identify the best geographic effect model, a null model (intercepts, random effects only), and three exploratory models including quadratic covariate effects in each category. Among segments/years, pintail pair counts ranged from 0–416 with a median value of 7.

A better model fit was obtained using PONDINDEX versus PDSI as the annual moisture index in the initial wetland-moisture model (ΔAIC = 2,523). The best approximating wetland-moisture model included all terms except the PONDINDEX*WETHA interaction in the non-zero count model (Table 3.3). As expected, wetland area, wetland count, and annual moisture index had, in general, positive effects on pintail pair counts with several modifying interactions (Table 3.3). Pintail counts demonstrated different relationships with wetland area between Canada and the USA; counts generally declined with increasing wetland area in Canada while counts demonstrated a positive asymptotic increase with wetland area in the USA. Similar counts per wetland area in both countries only occurred when transect wetland area was above ~150 ha. Further, pintail count response to wetland area varied with PPRPOP; as PPRPOP

increases, pintails show a greater response to wetland area in the low range and little, or a declining, relationship with wetland area above ~100 ha.

An interaction with COUNTRY indicated a slightly stronger response to wetland counts in the low range in Canada, and interactions with PONDNDX and PPRPOP demonstrated pintail count responded to wetland count at a greater rate under wetter conditions and at higher PPR populations. Pintail counts were only weakly dependent on the previous year's moisture.

Between alternate land-use models, PCTCROP provided a better fit to the data than did PCTGRASS (ΔAIC = 58), as did inclusion of the nonlinear form of PCTCROP (ΔAIC = 25; Table 3.4). Pintail counts showed an overall positive relationship with PCTCROP and a strong interaction with PPR population size. Pintails showed little response to the amount of crop when PPR population was low but settled at higher numbers in high cropland landscapes when PPR populations were high (Table 3.5, Figure 3.3).

Between alternate landform models, CVSRTM provided a better fit than did MEANSLOPE (ΔAIC = 54), and inclusion of the quadratic form of CVSRTM greatly improved fit (ΔAIC = 12; Table 3.4). Pintail count declined strongly as variation in elevation increased and this was strongly affected by PPRPOP; at low population, variation in elevation had little effect on pintail settling whereas at high population levels, pintails settled in much higher numbers in flatter landscapes (Table 3.5, Figure 3.4).

As expected, pintail counts were strongly influenced by location within the PPR with the exploratory model containing quadratic effects for latitude and longitude providing a better fit to the data than linear effects (ΔAIC=149; Table 3.4). Pintail counts vary geographically in the PPR such that highest counts generally occur at mid-latitudes in the western half of the region (Table 3.5, Figures 3.5a,b). Geographic variation in pintail counts within the PPR was informed

by an interaction between latitude and longitude (Table 3.5) such that pintails in the eastern PPR showed a low peak abundance in the Dakotas, pintails in the central PPR showed a high peak abundance near the 49th parallel, and pintails in the western PPR were most abundant in the central part of Alberta (Figure 3.5c). There was no strong evidence of shifting distributions east-west or north-south as PPR pintail population increased (Figure 3.5a,b).

3.5 Discussion

Fretwell and Lucas (1969) postulated that, while individuals will initially select habitats that confer the highest fitness available, thereafter density within and among patches will be adjusted so that all individuals experience similar fitness regardless of habitat choice (i.e., the "ideal free" distribution). Similarly, Brown (1969) postulated a 'buffer effect' model, where patch fitness does not decline with density, but patch density is limited and individuals are forced into habitats of lower fitness at high populations resulting in lower overall fitness (e.g., Potts et al. 1980, Pulliam et al. 1992). In the latter case, density-dependence is observed not at the patch scale but at the landscape scale (Pulliam 1996). Under the buffer model, it follows that the proportion of the population occurring in low fitness patches or landscapes will increase when populations are high (similar to the Fretwell-Lucas "ideal dominance" distribution). Rodenhouse et al. (1997) expanded and generalized this theme to embrace spatial heterogeneity; a mechanism they termed 'site-dependent' regulation of populations. Buffer or site-dependent models of habitat selection have inherent appeal when addressing breeding range and landscape-scale association in pintails, given demonstrated demographic consequences of their migratory settling patterns (e.g., Hestbeck 1995). A large-scale density-dependent buffer effect has been clearly demonstrated for migratory black-tailed godwit (*Limosa limosa islandica*) wintering in Britain, where use of lower quality estuaries increased the greatest as population size increased (Gill et al. 2001).

Here, I have attempted to evaluate how breeding habitat suitability within the PPR may be related to wetlands, land use, landform, and geographic patterns in distribution by relying on pintail harvest and population distribution data. My underlying assumption was that site-dependent habitat associations within the PPR that increase recruitment will translate directly to the population level. I believe this to be a reasonable assumption given the recognized importance of the PPR to breeding ducks in general (Batt et al. 1989) and the overflight effect specifically (Smith 1970, Henny 1973, Derksen and Eldridge 1980).

Pintails are characterized as 'nomadic' in their settling patterns during the breeding season, often following climatic variation in local wetness (Austin and Miller 1995). My results indicate that this behaviour, examined at several scales, affects reproductive success. The effect of PPR pintail population size on population-level recruitment that I observed has been described previously and has been attributed to a 'drought-displacement' of pintails into boreal and arctic regions where reproductive success is thought to be lower (Calverley and Boag 1977, Hestbeck 1995, Grand and Flint 1996a; but see Flint and Grand 1996). When the PPR is generally wet, pintails may settle to breed earlier, expend less energy in nutrient acquisition, expend greater effort in breeding during a relatively longer breeding season, lay larger clutches, and experience greater reproductive success than possible in more northern environments (Calverley and Boag 1977, Krapu et al. 1983, Kokko 1999, Krapu et al. 2000). Furthermore, female survival is reduced during wet years due to increased breeding effort, further inflating recruitment estimates from the fall harvest (Dufour and Clark 2002, Devries et al. 2003, Arnold et al. 2012). Thus, the overall wetness of the PPR appears to affect the attractiveness and carrying capacity of the region for pintails and their reproductive success as well (Raveling and Heitmeyer 1989, Runge and Boomer 2005, this study). This represents an example of site-dependent population

regulation at the breeding range scale in a migratory bird (similar to that reported by Gill et al. 2001) mediated by a climate-induced effect on carrying capacity in the more suitable habitat.

My results suggest that at the population level, recruitment of pintails was affected by the distribution of pintails within the PPR relative to certain landscape characteristics. Thus, these characteristics may be viewed as indicators of landscape suitability and used to test adaptive landscape association. When pintails settle in association with locations that are wetter than normal (i.e., high PDSI or PONDINDEX), recruitment tends to be greater, although for PONDINDEX, this effect was most pronounced when PPR populations were high. This effect clearly suggests a fitness advantage of selecting wetter than normal landscapes and suggests an explanation for the pintail's nomadic nature (e.g., Hochbaum and Bossenmeier 1972, Krapu et al. 1983). Similar phenomena occur elsewhere where waterbirds occupy breeding ranges with highly variable wetland conditions (Roshier et al. 2002, Petrie and Rogers 1997). The underlying mechanism driving this effect may be an earlier and greater breeding effort by adults, or greater food and habitat availability for both adults and young in wetter locations (Krapu et al. 1983, Cowardin et al. 1985, Greenwood et al. 1985). Alternatively, concentrations of pintails and other ducks in wetter than normal locations may swamp local predators as suggested in Chapter 2, or benefit from lower predation as a result of locally abundant alternate primary prey (Yang et al. 2010, Walker et al. 2013).

As predicted, population-level recruitment index was higher when pintails demonstrated a greater association with landscapes containing relatively more grassland habitat. However, the corresponding prediction that recruitment would be lower when pintails had greater association with landscapes containing more cropland was not supported. The amount of grassland generally has strong positive effects (and cropland, negative effects) on waterfowl nest survival

at landscape scales (Greenwood et al. 1995, Horn et al. 2005, Stephens et al. 2005), and nest survival is the vital rate most influential in waterfowl recruitment rate (Hoekman et al. 2002, Koons et al. 2006). However, high grassland may have negative effects on duckling survival where brood density is elevated (Gunnarsson et al. 2006, Amundson and Arnold 2011, but see Bloom et al. 2012). Counteracting effects on nest versus duckling survival at the landscape scale may explain the weak effects of land use covariates at a regional scale. There was no evidence that the relationship varied with PPR population size suggesting no density-dependence effects.

Landform characteristics associated with pintail settling in the PPR appeared to have a strong influence on population-level recruitment. Recruitment tended to increase with average slope but also to be maximized when pintails predominantly settle in landscapes with moderate variation in elevation. This presents somewhat of a conundrum given that these covariates were highly correlated. A possible explanation is that landscapes of moderate elevational variation contain an optimum mix of seasonal and semipermanent/permanent wetlands. Landscapes at the extremes of elevational variation may, 1) dry out or drain rapidly (i.e., if very flat with shallow seasonal wetlands) thus providing limited brood-rearing habitat in early summer, or 2) maintain abundant and stable predator populations detrimental to recruitment (i.e., in rolling topography with many semipermanent and permanent wetlands; e.g., Krapu et al. 2004, Walker et al. 2013). Thus, conditions that distribute pintails into flatter landscapes could have a negative effect on recruitment contrary to my original prediction of higher recruitment in flatter landscapes. The combination of wetland types preferred by pintails and some indication that flatter landscapes are more prone to cultivation (Herfindal et al. 2012) may create conditions favorable for ecological or evolutionary traps when these landscapes are wet (Best 1986, Miller and Duncan 1999,

Richkus 2002). There was no evidence in the data that recruitment response to pintail distribution relative to landform varied with population size.

Surprisingly, geographic location within the PPR, or population-mediated shifts in location within the PPR, seemed to have no effect on population-level recruitment despite known latitudinal and longitudinal gradients in waterfowl nest success and survival linked to gradients in predator communities (Sargeant et al. 1993, Reynolds et al. 2001, Devries et al. 2003, DUC unpublished data). Distribution of pintails within the PPR can vary greatly from year to year and much of the post-1980 decline in pintail numbers coincided with declining numbers settling in the northern 'Parkland' fringe of the PPR; shifting the population distribution further south within the PPR (Miller and Duncan 1999). Despite this shift, recruitment indices have remained relatively stable throughout (Miller and Duncan 1999). Coincident declines in summerfallow in the southern western Canadian PPR during this period may have offset any gains in recruitment a southern distribution may have conferred, but evidence for this is circumstantial (Carlyle 1997, Podruzny et al. 2002).

The patterns in recruitment outlined above provide reasonable indices of landscape suitabilities available to pintails in the PPR. Many uncertainties remain, especially regarding the interplay of landscape characteristics and the specific vital rates that comprise recruitment. Regardless, these results set the stage for examining potential adaptive patterns in the association of pintails with landscape characteristics as mechanisms of density and site-dependent population regulation (Brown 1969, Fretwell and Lucas 1969, Pulliam 1996, Rodenhouse et al. 1997, Gill et al. 2001).

Habitat association models examined in my analysis quantified the effect of spatially varying habitat features, climatic variation, population size, and their interactions on landscape

use by pintail pairs within the PPR. As expected, pintail pair numbers demonstrated a positive asymptotic increase with wetland area and wetland count such that change in pair numbers per unit increase in wetland area and abundance was greatest where area and abundance were small. This may be a reflection of greater pintail response to smaller wetlands observed at the basin scale (e.g., Cowardin et al. 1995, Bartzen 2008). Greater use of smaller basins is likely a result of greater pair isolation opportunity and more food resources per unit area than found on larger basins (Dzubin 1969b, Armstrong and Nudds 1985).

Annual wetness, PPR population size, and country all affected pintail response to wetland area and counts. Pintail pairs were much more numerous when local conditions were relatively wet but they were much less responsive to the previous year's moisture; a pattern in keeping with their 'nomadic' nature in response to moisture (Austin and Miller 1995). Annual wetness further moderated pintail response to wetland count; pintails showed much higher response to wetland count under wetter conditions. Pintail population size in the PPR moderated pintail response to both wetland area and wetland count. At high PPR population, pintails showed a stronger response to lower wetland area and higher wetland counts characteristic of landscapes with many small basins. The strong effect of annual wetness and PPR population size on pintail response to wetland area and count is likely a combination of annual wetness effects on the availability and quality of wetlands (i.e., both space [size and number] and wetland associated food [invertebrates and seeds]; Stewart and Kantrud 1973, 1974, Krapu 1974), as well as larger-scale effects such as decisions about whether to settle in the PPR at all during dry years (Smith 1970, Hestbeck 1995). These responses seem consistent with adaptive choices given chances of increased reproductive effort and success in wet versus dry years (Krapu et al. 1983, Cowardin et al. 1985, this analysis)

and increased recruitment when more pintails settle in the PPR (Runge and Boomer 2005, this analysis).

Pintails showed different responses to wetland area and count in Canada versus the USA. In Canada, pintail pairs were much higher at low wetland area (suggesting settling at higher density) and declined as wetland area increased. In the U.S., pintail pair numbers showed positive asymptotic growth with wetland area equalizing with Canada above 250 ha per survey segment. Pintail pairs were higher per wetland count and increased with wetland count at a greater rate in the low range in prairie Canada versus the US, such that pintails per wetland were higher across the board in the Canadian PPR. This result is consistent with the analysis of Miller and Duncan (1999) which showed higher pintail density per pond in prairie Canada versus prairie U.S. Despite different data sources used to quantify wetland area and count per survey segment, median estimates were similar between countries (Canada: area = 74.9 ha, count = 104.7; USA: area = 75.7 ha, count = 87.5). Regardless, I suggest considering wetland area and counts for Canada as indices given the modeled derivation of the data, as opposed to the high-resolution digitized wetland data available for U.S. wetlands.

The models I examined of pintail pair associations with land use indicated that pintail pairs were not associated with the amount of cropland in the landscape at low PPR population, but that pairs showed a stronger association with cropland landscapes when PPR populations were high. This finding is similar to results in Chapter 4 that, when selecting nest sites among habitats available, the probability of nesting in spring-seeded cropland (low nest survival) was greater in landscapes with high pintail density. Given evidence that nest survival tends to be lower in landscapes with more cropland and less grassland (e.g., Stephens et al. 2005), this pattern suggests a landscape-level buffer or site-dependent effect with respect to land use that may

negatively affect recruitment rate. My analysis showing a positive effect on recruitment when PPR pintails show higher association with grassland is consistent with this general conclusion.

Greater association of pintails with cropland landscapes only at high pintail population size does not support an ecological trap hypotheses (e.g., Miller and Duncan 1999, Richkus 2002); however, the pattern may be consistent with an evolutionary trap (Schlaepfer et al. 2002) if pintails respond to characteristics of cropland-dominated landscapes (flatter, shallow wetlands) when these landscapes are wet. My analysis ignored finer scale land use changes, like changes in cropping practices over time; however, my analysis is likely conservative in its conclusions assuming that cropland has become less suitable for nesting pintails over time (e.g., Podruzny et al. 2002).

Population size similarly affected pintail associations with landform such that pintails showed little association with elevation variation when PPR populations were low but showed a strong association with flatter landscapes when relatively more pintails settle in the PPR. As previously noted, flatter landscapes likely contain more seasonal wetlands and may contain more cropland (Stewart and Kantrud 1973, Krapu 1974). Because PPR pintail populations generally increase in wetter years, this may simply reflect opportunistic response to newly available habitat (e.g., Walker et al. 2013). The shift may be adaptive if there are benefits associated with opportunistic use of a variably available environment, especially temporary and seasonal wetlands, as noted by previous authors (Hochbaum and Bossenmeier 1972, Stewart and Kantrud 1973, Johnson and Grier 1988). However, my recruitment analysis suggests highest recruitment occurs when the PPR population is centered in the middle of the observed range of elevation variation (0.017-0.018 CVSRTM; Fig. 2f), as discussed above. Therefore, conditions that shift the population into flatter landscapes would be expected to decrease recruitment within the PPR.

Thus, greater use of flatter landscapes as the PPR population size increases suggests a landscape-level buffer or site-dependent effect as seen above with land use. This may seem somewhat at odds with increasing recruitment observed as the PPR population increases as observed, but I suspect this is due to effects at different scales; a population distribution effect between the PPR and Alaska/northern Canada as described previously, versus an addition effect of distribution within the PPR.

Lack of clear recruitment consequences of geographic distribution (LAT, LONG) within the PPR reduce the ability to interpret geographic habitat associations from an adaptive standpoint. Pintail pairs showed the greatest association with landscapes in southwestern Saskatchewan and southcentral Alberta, a pattern that has been noted by previous authors (e.g., Bellrose 1980), and in previous analyses of these data (Johnson and Grier 1988, Podruzny et al 2002). This region is best characterized as the Mixed Grassland ecoregion in prairie Canada and the Northwestern Glaciated Plains in the US and includes wetland-rich morainal features like the Missouri Coteau of Saskatchewan and North Dakota. In a broad sense, and more so than in other ducks, this distribution corresponds to gradients in waterfowl nest success (i.e., higher to the south and west in the PPR; Reynolds et al. 2001, DUC unpublished data). Increasing PPR population size accentuates, but does not geographically shift, this broad geographic pattern suggesting strong inherent affinities for regional landscape characteristics.

In summary, my analysis uncovered new information about the recruitment consequences of pintail landscape associations within the PPR suggesting possible adaptive responses to landscape characteristics reflecting potential for improved reproductive success. Population-level recruitment tended to be higher when pintails in the PPR settled in landscapes that were wetter than normal, contained more grassland, and were moderately variable in elevation.

Pintails showed strong association with wetter than normal landscapes suggesting an adaptive response. Pintails were positively associated with the amount of cropland in the landscape when pintail populations were high which may be a buffer response shifting pintails into habitat with lower reproductive potential (i.e., lower grassland). Pintails were more associated with flatter landscapes when populations were high suggesting either opportunistic use of increased seasonal wetlands in these landscapes, or a buffer response shifting pintails into landscapes with lower reproductive success. Broad geographic associations indicated pintails were most abundant in southwestern Saskatchewan and south-central Alberta with no evidence that shifts in geographic distribution were associated with population-level recruitment. On balance, my results indicate that pintails in the PPR express adaptive habitat associations with density-dependent mechanisms possibly acting through buffer or site-dependent shifts in landscape association. Further examination and experimental tests of spatial and behavioural mechanisms operating at the level of nest and landscape selection are needed to more fully understand the evolutionary significance of habitat choice in this species, including potential interspecific interactions.

While of theoretic utility, the insights provided above, along with information on patterns of nest habitat preference and reproductive success from Chapter 2, also have applied utility for informing species conservation efforts. In the following chapter, I integrate results from these chapters to construct models of average pintail population distribution and reproductive success given location and land use characteristics within the PPR. These tools can be used to target conservation efforts and predict the consequences of habitat conservation and management activity.

Table 3.1. Covariate models outperforming the null model examining the relationship between annual pintail population recruitment indices and PPR population-weighted landscape covariates in the Prairie Pothole Region, 1961–2003. Best-approximating models in each covariate model suite are highlighted in **bold** if they outperform the best-approximating population size model highlighted in grey. ΔAIC_c values are provided relative to the best-approximating population size model highlighted in grey.

Model	-LL	k	AIC_c	ΔAIC_c
Annual Moisture Models				
PPRPOP PPRPOP^2 WGTPOND WGTPOND^2 PPRPOP*WGTPOND	**-6.55**	**7**	**30.50**	**1.78**
PPRPOP PPRPOP^2 WGTPOND	-10.59	5	32.90	
PPRPOP PPRPOP^2 WGTPOND WGTPOND^2	-9.55	6	33.58	
WGTPDSI	**-11.67**	**3**	**29.98**	**2.30**
PPRPOP WGTPDSI	-11.15	4	31.41	
PPRPOP PPRPOP^2 WGTPDSI	-10.03	5	31.78	
PPRPOP PPRPOP^2 WGTPDSI PPRPOP*WGTPDSI	-9.84	6	34.16	
PPRPOP PPRPOP^2 WGTPDSI WGTPDSI^2 PPRPOP*WGTPDSI	-8.91	7	35.21	
Landuse Models				
PPRPOP PPRPOP^2 WGTCROP	-11.17	5	34.06	
PPRPOP PPRPOP^2 WGTCROP PPRPOP*WGTCROP	-10.93	6	36.33	
PPRPOP PPRPOP^2 WGTCROP WGTCROP^2 PPRPOP*WGTCROP	-10.76	7	38.92	
PPRPOP PPRPOP^2 WGTGRASS	**-10.2**	**5**	**32.11**	**0.17**
PPRPOP PPRPOP^2 WGTGRASS PPRPOP*WGTGRASS	-9.79	6	34.04	
PPRPOP PPRPOP^2 WGTGRASS WGTGRASS^2 PPRPOP*WGTGRASS	-9.79	7	36.97	
Landform Models				
PPRPOP PPRPOP^2 WGTSLOPE	**-9.84**	**5**	**31.39**	**0.89**
PPRPOP PPRPOP^2 WGTSLOPE PPRPOP*WGTSLOPE	-9.17	6	32.81	
PPRPOP PPRPOP^2 WGTSLOPE WGTSLOPE^2 PPRPOP*WGTSLOPE	-8.88	7	35.16	
PPRPOP PPRPOP^2 WGTCVSRTM WGTCVSRTM^2	**-8.04**	**6**	**30.56**	**1.72**
PPRPOP WGTCVSRTM WGTCVSRTM^2	-9.77	5	31.26	
WGTCVSRTM WGTCVSRTM^2	-12.05	4	33.22	
PPRPOP PPRPOP^2 WGTCVSRTM WGTCVSRTM^2 PPRPOP*WGTCVSRTM	-7.93	7	33.24	
Geographic Distribution Models				
PPRPOP PPRPOP^2 WGTLAT	-11.45	5	34.61	
PPRPOP PPRPOP^2 WGTLAT WGTLAT^2	-10.58	6	35.64	
PPRPOP PPRPOP^2 WGTLAT WGTLAT^2 PPRPOP*WGTLAT	-10.57	7	38.54	
PPRPOP PPRPOP2 WGTLONG	-11.08	5	33.88	
PPRPOP PPRPOP2 WGTLONG WGTLONG2	-10.85	6	36.16	
PPRPOP PPRPOP2 WGTLONG WGTLONG2 PPRPOP*WGTLONG	-10.75	7	38.90	
PPRPOP PPRPOP^2 GEO_PC1	-11.55	5	34.81	
PPRPOP PPRPOP^2 GEO_PC1 GEO_PC1^2	-10.94	6	36.35	
PPRPOP PPRPOP^2 GEO_PC1 GEO_PC1^2 PPRPOP*GEO_PC1	-10.9	7	39.20	
Population Size Models				
PPRPOP PPRPOP^2	**-11.58**	**4**	**32.28**	**0.00**
PPRPOP	-13.06	3	32.77	
NULL Model	-16.18	2	36.67	

Table 3.2. Best-approximating model parameter estimates and standard errors (SE) for covariates in the population size, annual moisture, land use, landform, and geographic models predicting annual pintail population recruitment indices, 1961–2003.

Parameter	Estimate	SE
PPRPOP	0.055	0.024
$PPRPOP^2$	-0.0010	0.0006
PPRPOP	-0.128	0.070
$PPRPOP^2$	-0.0020	0.0007
WGTPOND	2.90	1.06
$WGTPOND^2$	-0.141	0.051
PPRPOP*WGTPOND	0.020	0.008
WGTPDSI	0.108	0.034
PPRPOP	0.064	0.024
$PPRPOP^2$	-0.0010	0.0006
WGTGRASS	3.39	2.00
PPRPOP	0.067	0.024
$PPRPOP^2$	-0.0013	0.0006
WGTSLOPE	1.86	0.97
PPRPOP	0.054	0.023
$PPRPOP^2$	-0.0010	0.0005
WGTCVSRTM	75.76	27.96
$WGTCVSRTM^2$	-21.46	7.98

Table 3.3. Best-approximating model coefficient estimates, standard errors (SE), and index of importance (coefficient of variation [CV]) for covariates in the best-approximating wetland-moisture model predicting pintail pair numbers on survey segments across the PPR of North America, 1961–2009. Given the zero-inflated modeling approach, each parameter may be represented in both zero-count probability and non-zero count model components.

EFFECT	Estimate	SE	CV
Zero-count probability model			
SEGAREA	0.658	0.263	0.400
PPRPOP	-2.081	0.370	0.178
COUNTRY	-1.526	0.376	0.246
WETHA	-0.860	0.258	0.300
$WETHA^2$	0.051	-0.017	0.333
WETCNT	0.817	0.231	0.283
$WETCNT^2$	0.046	0.016	0.348
PONDINDEX	-9.368	0.703	0.075
$PONDINDEX^2$	1.147	0.088	0.077
PONDINDEXLAG1	-0.239	0.054	0.226
PONDINDEX*WETHA	-0.116	0.058	0.500
PONDINDEX*WETCNT	-0.392	0.061	0.156
COUNTRY*WETHA	0.444	0.103	0.232
COUNTRY*WETCNT	-0.230	0.080	0.348
PPRPOP*WETHA	0.180	0.024	0.133
PPRPOP*WETCNT	-0.057	0.021	0.368
PPRPOP*PONDINDEX	0.229	0.112	0.489
Non-zero-count model			
SEGAREA	-0.334	0.116	0.347
PPRPOP	0.727	0.108	0.149
COUNTRY	1.701	0.171	0.101
WETHA	0.764	0.083	0.109
$WETHA^2$	-0.041	0.008	0.195
WETCNT	-0.088	0.071	0.807
$WETCNT^2$	-0.016	0.007	0.438
PONDINDEX	1.911	0.195	0.102
$PONDINDEX^2$	-0.254	0.025	0.098
PONDINDEXLAG1	0.046	0.017	0.369
PONDINDEX*WETCNT	0.110	0.014	0.127
COUNTRY*WETHA	-0.269	0.047	0.175
COUNTRY*WETCNT	-0.059	0.035	0.593
PPRPOP*WETHA	-0.079	0.010	0.127
PPRPOP*WETCNT	0.018	0.007	0.389
PPRPOP*PONDINDEX	0.094	0.031	0.330

Table 3.4. Land-use, landform, and geographic covariate models as additions to the best-approximating wetland-moisture model (WETMODEL) predicting survey segment-level pintail pair count in the Prairie Pothole Region, 1961–2009. Alternate models (e.g., Alternate 1) test performance of alternate covariates as full models (best-approximating is highlighted in italics). 'A' and 'B' terms in the model reduction steps refer to the zero-count probability, and non-zero count model components, respectively, from which the term was removed. 'Exploratory' denotes the term added to the best-approximating model identified by model reduction (model in **bold**).

Model	-2LL	k	AIC
Land-Use			
Alternate 1: WETMODEL + PCTGRASS + PCTGRASS*PPRPOP	241166.0	43	241252.0
*Alternate 2: WETMODEL + CROP + CROP*PPRPOP*	*241108.0*	*43*	*241194.0*
Remove A PPRPOP*WETCNT	241110.0	41	241192.0
Remove B COUNTRY*WETCNT	**241112.0**	**40**	**241192.0**
Remove A PONDINDEX*WETHA	241117.0	39	241195.0
Exploratory: add $PCTCROP^2$ to best	241083.0	42	241167.0
Landform			
Alternate 1: WETMODEL + MEANSLOPE + MEANSLOPE*PPRPOP	241098.0	43	241184.0
*Alternate 2: WETMODEL + CVSRTM + CVSRTM*PPRPOP*	*241044.0*	*43*	*241130.0*
Remove B COUNTRY*WETCNT	241045.0	42	241129.0
Remove B PPRPOP*WETCNT	**241046.0**	**41**	**241128.0**
Remove A PONDINDEX*WETHA	241050.0	40	241130.0
Remove A PPRPOP*PONDINDEX	241054.0	39	241132.0
Exploratory: add $CVSRTM^2$ to best	241030.0	43	241116.0
Geographic			
WETMODEL + LAT + LONG + LAT*LONG + LAT*PPRPOP + LONG*PPRPOP	240608.0	49	240706.0
Remove A $WETHA^2$	240608.0	48	240704.0
Remove A B SEGAREA	**240610.0**	**46**	**240702.0**
Remove B PPRPOP*LAT	240613.0	45	240703.0
Remove B PONDINDEXLAG1	240615.0	44	240703.0
Remove A PONDINDEX*WETHA	240618.0	43	240704.0
Remove A PPRPOP*WETCNT	240621.0	42	240705.0
Exploratory: add LAT^2 + $LONG^2$ to best	240453.0	50	240553.0
NULL	257042.0	6	257054.0

Table 3.5. Best-approximating model parameter estimates, standard errors (SE), and index of importance (coefficient of variation [CV]) for covariates in the best approximating land-use, landform, and geographic models predicting survey segment-level pintail pair count in the Prairie Pothole Region, 1961–2009. Given the zero-inflated modeling approach, each parameter may be represented in both zero-count probability and a non-zero count model components.

EFFECT MODEL	Estimate	SE	CV
Landuse Model			
Zero-count probability model			
PCTCROP	-0.197	0.620	3.147
$PCTCROP^2$	1.55	0.587	0.378
PPRPOP*PCTCROP	-0.579	0.092	0.159
Non-zero-count model			
PCTCROP	-0.663	0.268	0.404
$PCTCROP^2$	0.361	0.259	0.717
PPRPOP*PCTCROP	0.208	0.032	0.154
Landform Model			
Zero-count probability model			
CVSRTM	1.81	0.567	0.313
$CVSRTM^2$	0.220	0.066	0.300
PPRPOP*CVSRTM	0.126	0.043	0.341
Non-zero-count model			
CVSRTM	-0.843	0.248	0.294
$CVSRTM^2$	-0.114	0.029	0.254
PPRPOP*CVSRTM	-0.135	0.015	0.111
Geographic Model			
Zero-count probability model			
LAT	-24.82	5.00	0.201
LAT2	7.00	0.91	0.130
LONG	-22.86	3.84	0.168
$LONG^2$	1.93	0.21	0.109
LAT*LONG	-3.77	0.69	0.183
LAT*PPRPOP	-1.27	0.13	0.102
LONG*PPRPOP	-0.112	0.064	0.571
Non-zero-count model			
LAT	6.16	2.11	0.343
LAT2	-3.03	0.39	0.129
LONG	12.09	1.63	0.135
$LONG^2$	-1.07	0.09	0.084
LAT*LONG	2.14	0.30	0.140
LAT*PPRPOP	0.079	0.049	0.620
LONG*PPRPOP	0.167	0.022	0.132

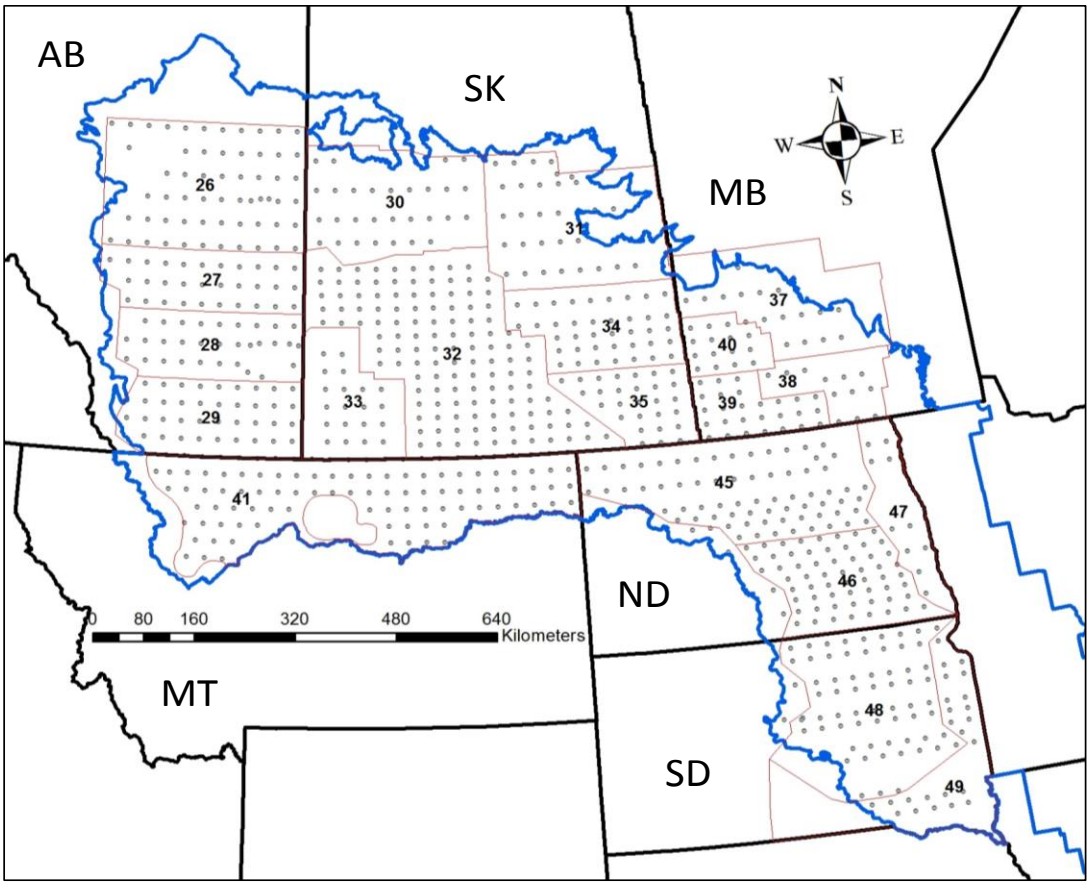

Figure 3.1. Extent and location of 809 May Waterfowl Breeding Population and Habitat Survey (WBPHS) survey segments (centroids:dots) within 20 survey strata (numbered polygons) located throughout the Prairie Pothole Region (PPR; outlined in blue) of Canada (AB, SK, MB) and the United States (MT, ND, SD).

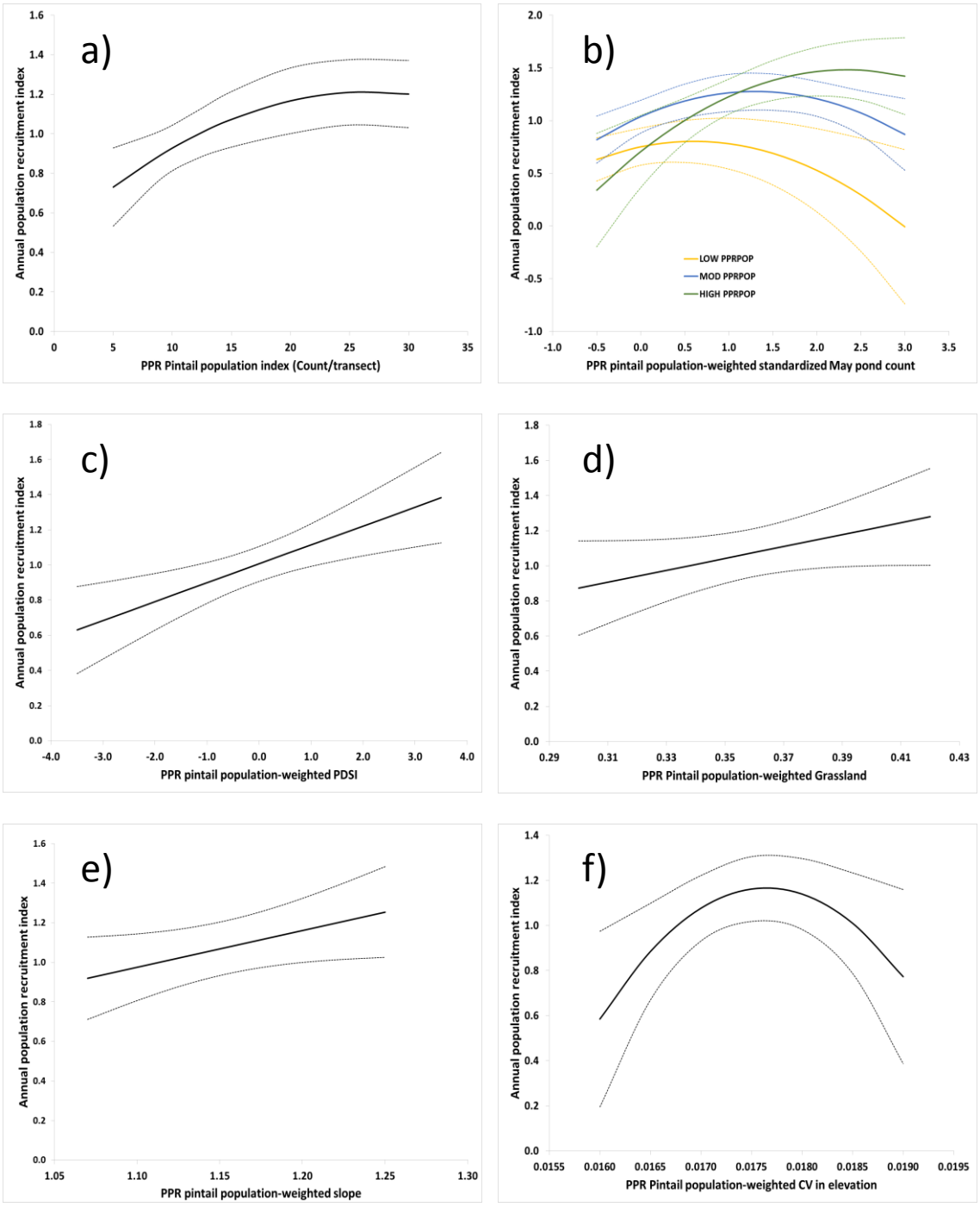

Figure 3.2. Relationships between annual pintail population recruitment indices and a) Prairie Pothole Region (PPR) pintail population size index, b) population-weighted May pond count index at low, moderate and high pintail population, c) population-weighted Palmer Drought Severity Index (PDSI), d) population-weighted proportion of grassland in the surrounding landscape, e) population-weighted mean slope of the surrounding landscape, and f) population-weighted coefficient of variation in elevation in the surrounding landscape within the PPR of North America, 1961–2003.

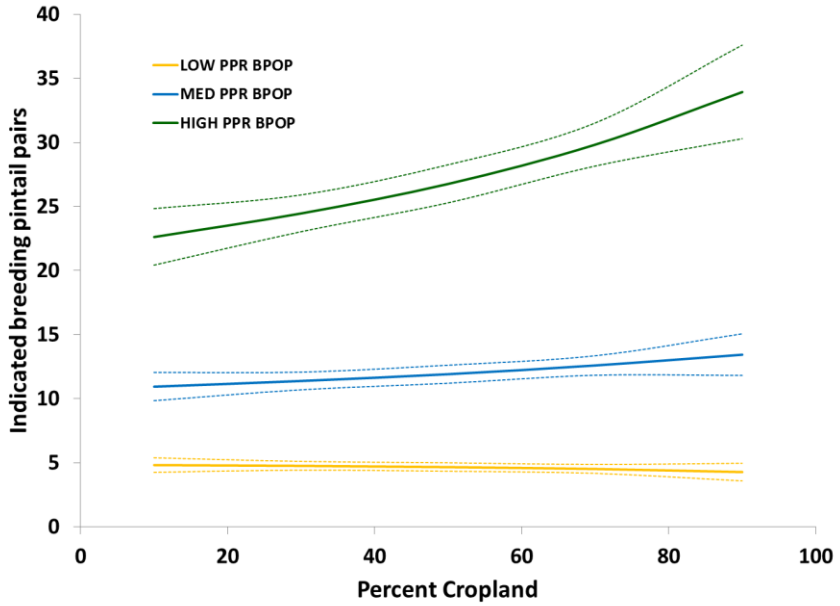

Figure 3.3. Relationship between pintail breeding pair counts and landscape-level percent cropland at low, medium, and high pintail population size estimates within the Prairie Pothole Region, 1961–2009.

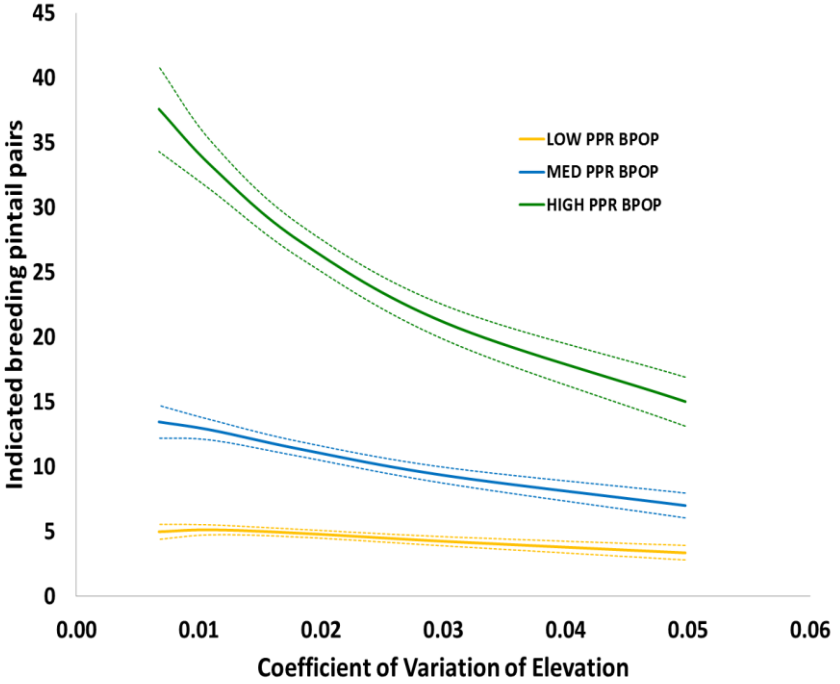

Figure 3.4. Relationship between pintail breeding pair counts and variation in Shuttle Radar Topography Mission (CVSRTM) elevations within a 41 km2 neighborhood around survey segment centroids at low, medium, and high pintail population size estimates within the Prairie Pothole Region, 1961–2009.

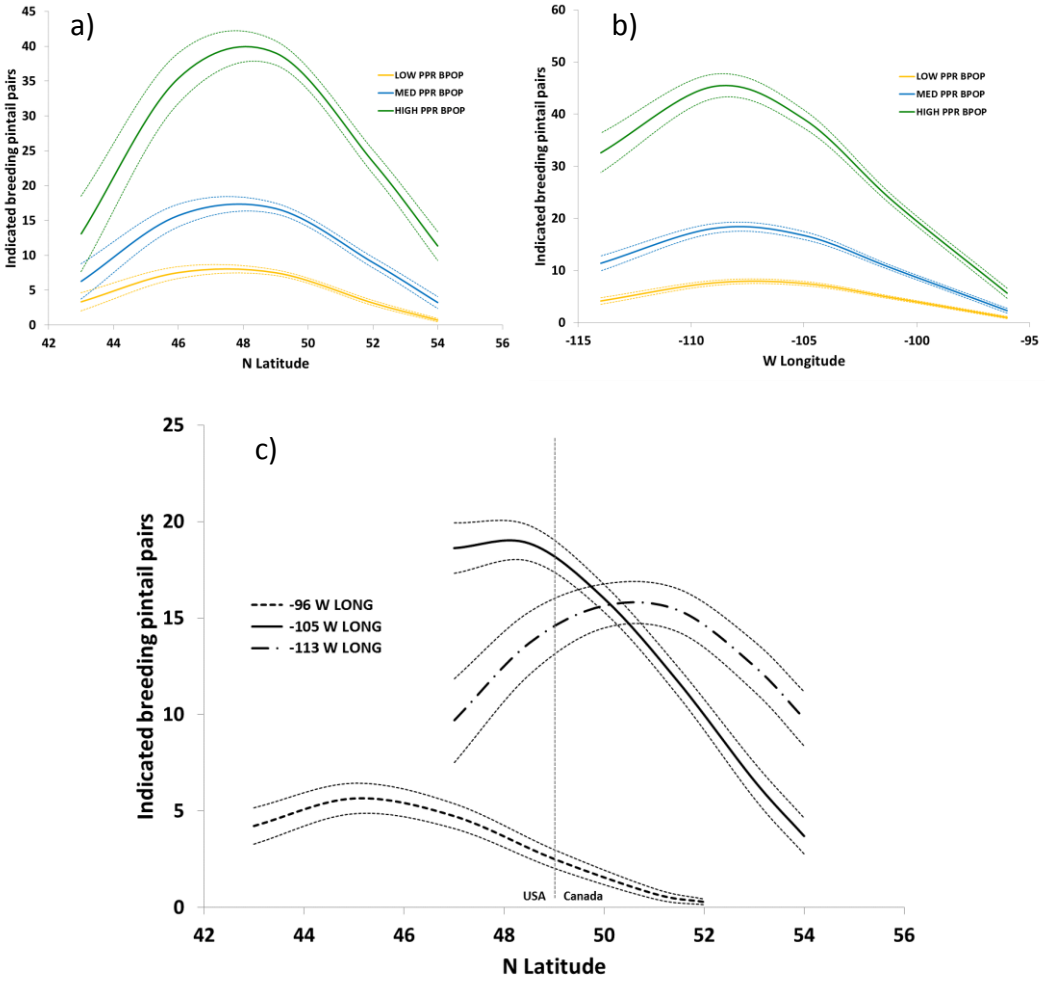

Figure 3.5. Relationships between pintail breeding pair counts and a) latitude at low, medium, and high pintail population size estimates, b) longitude at low, medium, and high pintail population size estimates, and c) the interaction of latitude and longitude within the Prairie Pothole Region of North America 1961–2009. The vertical dashed line in c) represents the location of the Canada-U.S. border.

CHAPTER 4. MODELLING NORTHERN PINTAIL DISTRIBUTION AND PRODUCTIVITY: TOOLS FOR CONSERVATION PLANNING IN THE PRAIRIE POTHOLE REGION OF NORTH AMERICA

4.1 Introduction

The glaciated region of central North America, also known as the Prairie Pothole Region (PPR), serves as the primary breeding area for many of North America's waterfowl (Batt et al. 1989). Historically, extensive grasslands and diverse wetlands provided ideal habitat for successful waterfowl reproduction in this region (Stephens et al. 2005). Since human settlement, however, a majority of the PPR has become an important agricultural production area for cereal grain, oil seed and row crops. Today, this region of North America is one of the most intensively cropped landscapes in the world (Foley et al. 2005). Conversion of grassland to annual cropland, and drainage and degradation of wetlands, has significantly altered the landscapes in which breeding waterfowl nest (e.g., Stephens et al. 2008), and represents the primary conservation concern for the North American Waterfowl Management Plan (NAWMP; Anonymous 1986).

Conversion of grasslands to cropland and associated alteration of predator communities in the PPR are thought to be the leading cause of long-term declines in waterfowl production in this region (Sargeant et al. 1993, Greenwood et al. 1995, Beauchamp et al. 1996, Stephens et al. 2008). In addition, the intensity of cropping practices has recently increased on existing cultivated lands. The largest and most economically and environmentally significant change in agricultural land use since the 1970s has been the decline in summer fallow, a practice where cropland is removed from production for alternate growing seasons for moisture accumulation, nitrogen release, and weed control (Carlyle 1997). In prairie Canada, the practice of summer fallowing declined by approximately 7.6 million ha from 1971 to 2011 (Statistics Canada 2011).

In its place, continuous cropping under minimum and zero-tillage practices with high nutrient and pesticide inputs has prevailed (Carlyle 1997). Ironically, these 'conservation tillage' practices, which leave more crop residue on the surface, in combination with continuous cropping, may create ecological traps for breeding birds (Best 1986). Podruzny et al. (2002) provided evidence that the decline in populations of northern pintail (*Anas acuta)* may have been the result of reduced nest survival as continuous cropping and minimum tillage replaced relatively safer nest sites in fallowed cropland (e.g., Best 1986).

Cropland conversion to grassland began occurring on marginal cropland in the U.S. under the Conservation Reserve Program (CRP) in the early 1990s (Reynolds et al. 2001). Conversion also began in Canada circa 1995 when removal of grain transportation subsidies made cropland less economically viable in some locations (Riemer 2005). Conversion of cropland to grassland (left idle or grazed/hayed) also has been a primary tool used by waterfowl managers under the North American Waterfowl Management Plan (NAWMP; Anonymous 1986) since the mid-1980s to increase nest survival in landscapes attracting high waterfowl densities (e.g., Duebbert and Lokemoen 1976). Recent trends, and long-term projections of cropland area, however, suggest that conversion of grassland to cropland is again on the rise as agricultural commodity prices put pressure on lands not in crop production in both Canada and the U.S. (Rashford et al. 2010, 2011, Wright and Wimberly 2013). While waterfowl have benefited greatly from programs like CRP and NAWMP programs (e.g., Reynolds et al. 2001), these benefits are expected to diminish as grasslands are converted to cropland (Stephens et al. 2008, Rashford et al. 2011).

Waterfowl are one of the most highly 'managed' groups of species in North America, combining both widespread management of wintering and breeding habitat and management of

population harvest rates (Nichols et al. 1995). Thus, understanding how species are exposed to habitat across their range, and how changing habitat will affect population carrying capacity and/or vital rates is critical to the habitat and harvest management nexus that embodies modern waterfowl management (e.g., Anderson et al. 2007, Mattsson et al. 2012).

Patterns of nest habitat preference and nest survival provide critical information for waterfowl conservation planning given their joint influence on waterfowl recruitment (e.g., Reynolds et al. 2001, Hoekman et al. 2002). Change in land use may disproportionally affect northern pintails given their propensity to nest in active croplands (Austin and Miller 1995). Exposure of nesting pintail hens and nests to agricultural disturbance is well documented (e.g., Goelitz 1918, Milonski 1958, Klett et al. 1988, Greenwood et al. 1995), however, quantifying agricultural impacts on pintail populations has been problematic. For instance, until recently, estimation of waterfowl exposure to agricultural disturbance has been hampered by incomplete estimates of relative nest habitat selection including use of annually cropped lands (e.g., Richkus 2002, Devries et al. 2008a).

For most waterfowl species in the PPR, conservation planning under the NAWMP is aimed at maintaining existing habitat and increasing nest success through restoration of high quality nesting habitat. Currently, a primary assumption is that pintail productivity (carrying capacity and nest success) in the PPR (especially the Canadian PPR) has declined over time. Wetland loss, especially loss of small, shallow, basins preferred by pintails, may have reduced the carrying capacity of the region to attract and hold pintail pairs (Bethke and Nudds 1995, Watmough and Schmoll 2007), and land use change may have reduced the ability of pintails to successfully hatch nests (Miller and Duncan 1999, Podruzny et al. 2002, Miller et al. 2003). Investments in conservation programs for pintails are believed to provide variable returns both

regionally and locally depending on the spatial and temporal overlap of pintails and conservation actions (Prairie Habitat Joint Venture [PHJV] Implementation Plan; http://phjv.ca/publications.html). Habitat conservation programs, by their nature, are typically fixed in geography and are expected to provide benefits over multiple years as a result of frequent use by target species. Therefore, to predict the effects of landscape change (including climate change), and the benefit of conservation actions, for highly mobile species like pintails requires models that integrate the interaction of species distribution, habitat selection, and a demographic response at multiple scales.

Therefore, my objectives are to incorporate modeling approaches developed at multiple scales in Chapters 2 and 3 to, 1) model and map the estimated long-term average spatial abundance of pintail pairs across the PPR as a function of landscape-level covariates, and 2) construct a deterministic model predicting pintail hatching success given estimates of nesting effort, habitat availability, habitat-specific nest site preferences and nest survival rates, and influential landscape characteristics. I focus on hatching success as this demographic rate is one of the most important determinants of recruitment potential in prairie nesting ducks (Hoekman et al. 2002). Thus, the product of this chapter will be a set of conservation planning tools that may be combined to predict changes in hatching success of pintails given changes in population and landscape contexts across the PPR. This modeling effort combines elements of species distribution modeling (SDM; Elith and Leathwick 2009) and population viability analysis (PVA; Beissinger and McCullough 2002). Spatially explicit population models of this type are becoming increasingly popular to aid in conservation efforts worldwide for a variety of taxa, most often endangered species (e.g., Kuemmerle et al. 2011, Franklin et al. 2014, Schumaker et al. 2014), but rarely at the scale examined here.

4.2 Study Area and Methods

4.2.1 Models of Pintail Pair Distribution

4.2.1.1 Study Area and Scope

I use several spatial and temporal datasets to examine the relationships between long-term pintail counts within the PPR and landscape-scale habitat and geographic covariates. I restricted my investigation to the PPR because this region is the primary breeding region for pintails in the midcontinent of North America, and detailed spatial datasets are readily available for this region. I limited investigation to the time period 1961–2009 because visibility-corrected pintail abundance estimates (see below) were available only from 1961 onward (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987). For this modeling effort, I define 'landscapes' as areas as small as the area contained in waterfowl survey segments (see below) but including up to the size of study sites used in Chapter 2 (41 km^2).

4.2.1.2 Pintail counts

I used pintail data collected as part of the Waterfowl Breeding Population and Habitat Survey conducted annually in May (MWBPHS; U.S. Fish and Wildlife Service and Canadian Wildlife Service 1987) along 809 systematically located permanent survey transect segments within 23 strata (strata 26–35, 37–41, and 45–49) of the PPR boundary in Canada and the U.S. (Figure 4.1). Survey transects are systematically spaced within strata, and each transect consisted of 2–11 survey segments, each ~29 km long and 0.4 km wide (11.6 km^2 in area). Procedures for conducting surveys and evaluations of their efficacy were described in detail by Bowden (1973) and Benning (1976).

Survey biologists record the numbers of all pintails seen from a fixed-wing aircraft flying ~160 km/h at 30–46 m AGL along survey transects. Species are counted as pairs (male and female in close association), lone males, grouped males <5, and groups (mixed-sex groupings in close association, and ≥ 5 males in a group). Concurrent with aerial waterfowl counts, biologists conduct complete ground surveys on a sub-sample of survey segments (~50) to establish visibility-correction factors which are applied to aerial counts at the stratum level (hereafter, visibility-corrected counts). Survey segment-level count data used in this analysis were downloaded from the USFWS Office of Migratory Bird Management online data portal (https://migbirdapps.fws.gov/). The survey segment was the experimental unit in my analyses. I used the segment-specific mean count of indicated breeding pintail pairs (i.e., visibility-corrected observed pairs + lone males + grouped males <5; Dzubin 1969a, Hammond 1969) as the response variable in my analysis of landscape-level habitat associations. I used mean values under the rationale that conservation actions are focused on the long-term number of waterfowl exposed to the action rather than the number exposed in any given year.

4.2.1.3 Spatial covariates

I selected covariates that were available across the PPR because my intent was to understand factors associated with the distribution of breeding pintails across the entire region, and also to extrapolate model estimates to the spatial extents of the PPR. Covariates were generally extracted within, or associated with, the boundary of the surveyed area of each survey segment in ArcGIS. I limit covariates examined to those included in the best-approximating model from Chapter 3.

Because ducks are wetland obligate species, I included the best available data for the spatial distribution of wetland numbers (count) and area (ha) for the PPR. In Canada, wetland count and

area were derived from digital hydrography and saturated soils features in the CanVec database (Edition 1.2.2; Natural Resources Canada 2011). Because CanVec hydrography fails to detect small wetland basins, I used overlapping CanVec and Ducks Unlimited Canada high-resolution wetland inventories for 1,371 – 41.4 km^2 blocks, and constructed separate wetland area and count adjustment models (i.e., DUC Inventory/CanVec; DUC unpublished data). Adjustment models included the effects of province, soil landscape variables (Canadian Soil Information System 2011; drainage, surface form, water holding capacity), and number and area of small CanVec basins (i.e., small = <0.5 ha; rationale: more basins are missed where there are many small wetland basins). The best-approximating adjustment models were then applied in ArcGIS to covariates extracted from all 41.4 km^2 blocks within prairie Canada. An adjusted wetland area and count surface was then created by multiplying raw CanVec wetland area and count by spatially coincident adjustment factors. Finally, estimated wetland area (WETHA) and count (WETCNT) were extracted from these adjusted wetland surfaces as the mean of pixel values within survey segment boundaries.

Within the U.S. PPR, wetland area and count were extracted along survey segments from the National Wetlands Inventory database (NWI; U.S. Fish and Wildlife Service 2011). No adjustments were made as NWI is a stand-alone high-resolution wetland-specific database. Because WETHA and WETCNT were taken from different sources in Canada and the USA, I included COUNTRY (USA/Canada) as a categorical variable interacting with each wetland variable to account for potential differences in pintail count response between countries.

I used land cover metrics to characterize the degree of agricultural intensity associated with survey segments, specifically the proportion of the local landscape comprised of annual cropland (PCTCROP). PCTCROP was estimated from digital land cover products produced by

Agriculture and Agri-Food Canada (AAFC; 2008) and the U. S. Geological Survey (USGS; Homer et al. 2007) representing land cover *circa* 2000 and 2001, respectively. In Canada, PCTCROP was defined as the proportion of the survey segment in the "Annual Cropland" category. In the U. S., PCTCROP was defined as the proportion of the survey segment in "Cultivated Crops". PCTCROP was extracted within survey segment boundaries using Spatial Analyst Zonal Statistics in ArcGIS.

Because pintails are generally recognized as being more prone to occupy flat to gently rolling topography than other ducks (Austin and Miller 1995), I used Shuttle Radar Topography Mission (SRTM3 Version 2; 3 arc-second resolution [~90 m], edited; Farr et al. 2007) digital elevation model (DEM) data to characterize landform surrounding survey segments. SRTM data represent the only DEM available for the entire PPR. I estimated the coefficient of variation in elevations within a 41 km^2 neighborhood using the mean and standard deviation of pixel elevation values generated with Spatial Analyst in ArcGIS. Subsequently, the mean of coefficient of variation pixel values (CVSRTM) was calculated from within survey segment buffers using Spatial Analyst.

I included latitude (LAT) and longitude (LONG) to account for previously described geographic trends in pintail counts (e.g., Bellrose 1980). LAT and LONG were defined by the location of the centroid of each survey segment.

4.2.1.4 Modeling Approach and Analysis

I modeled average pintail pair count on each survey segment as a function of covariates using negative binomial regression with a log-link in SAS (SAS Institute; PROC GENMOD). The negative binomial model explicitly estimates a dispersion parameter to accommodate unaccounted spatial covariance and other possible sources of overdispersion (White and Bennetts

1996). I used the 1961–2009 mean pintail pair count as the response variable for 809 survey segments with complete covariate data. WETHA and CVSRTM were transformed to normality with a natural log transformation and I applied a square-root transformation to WETCNT. I divided LAT and LONG by 10 to facilitate optimization in analytical procedures.

Given the observational nature of the data used in this analysis, I used information-theoretic techniques to select among competing models fit to the data (Johnson and Omland 2004). I began with a full model containing main covariates, the quadratic form of all continuous covariates, and plausible interactions between linear forms of covariates. I simplified models by sequentially removing the least-predictive covariate (i.e., the smallest F-ratio). Interaction terms and quadratics were always removed before associated main effects. I used Akaike's Information Criterion (AIC) adjusted for small samples (AIC_c, Burnham and Anderson 2002) to assess model fit. The model with the lowest AIC_c was identified as the best-approximating model. As this model was being developed as a predictive tool, I only considered the best-approximating model for making predictions.

To create the pintail pair distribution (pair density) surface for the PPR, I applied the best-approximating model using the Raster Calculator in ArcMap's Spatial Analyst. Specifically, covariate values were extracted from respective GIS layers within an 11.6 km^2 neighborhood (equal to the surveyed segment area), input into the model equation, and the estimated pair number assigned to a reference 400 m x 400 m pixel. Pair values in the final surface were recalculated to represent estimated pintail pairs/km^2 (note: estimated pintail pair density here represents the number of pintail pairs within a geographic unit [km^2] of space rather than a km^2 of wetland as used for the pintail density [PINDEN] covariate in previous chapters).

4.2.2 Models of Pintail Productivity

4.2.2.1 Study Area and Scope

I used data from three multi-year nesting studies conducted in prairie Canada by DUC (PHJV Assessment Study, 1993–2000; Pintail Study, 2005–2007; and Spatial/Temporal Variability Study [SPATS] 2001–2011) to model breeding pintail nest survival and nest site preference among common nesting habitats. PHJV Assessment Study areas were single sites, 64 km^2 in size, examined for 1 year only. Pintail Study and SPATS designs include clusters (hereafter, site clusters) of 6 – 41 km^2 study areas stratified by percent grassland composition, including 2 replicates each of low (< 30%), moderate (30-60%), and high (>60%) grassland area; each site cluster was examined for 1 or 2 years. In total, 63 study areas (1993–2011) were included in the grassland and parkland ecoregion (Figure 4.2).

Detailed physical descriptions of study areas, nest data collection methods, and data analysis procedures used in habitat preference and nest survival model development are provided in Chapter 2. Here, I incorporate the best-approximating models of factors affecting pintail nest habitat preferences and nest survival from Chapter 2, along with estimates of breeding propensity and renesting rates (from literature and expert opinion) to develop a deterministic predictive model estimating pintail hatching success given local habitat availability and landscape-level covariates.

4.2.2.2 Base Model Inputs

Base model inputs provide the landscape context in which the model will run and include important parameters that modify nest survival and nest site preference (see Chapter 2). Model inputs include the size of the planning landscape (km^2; typically 41 km^2 to match the scale of data acquisition used in model development), the number of breeding pintail pairs (females),

wetland area (km^2), and the proportion of each habitat (Table 4.1) within the planning landscape (i.e., habitat availability). I included two additional common habitats to those examined in Chapter 2; 'Other' (non-habitat; e.g., road surfaces, gravel pits, etc.), and 'Trees' (deciduous and coniferous groves). I include these habitats because they are common 'habitats' in the PPR but I assign values of 0 for preference because pintails did not typically use these habitats for nesting. Derived from these inputs are pintail pair density (PINDEN: pintail pairs/km^2 wetland), and the proportions of cropland (PCTCROP; sum of spring seeded and fall seeded cropland proportions) and grassland (PCTGRASS; sum of idle and grazed grassland and hayland proportions).

4.2.2.3 Habitat Selection

The best-approximating habitat selection model from Chapter 2 included standardized nest initiation date (IDATE) as a categorical variable (early, mid, late), habitat type, pintail pair density (PINDEN) and proportion grassland (PCTGRASS). The relative habitat preference for each habitat was estimated for early, mid, and late seasonal periods using base landscape covariate inputs in model estimating equations from Chapter 2 (Appendix C).

4.2.2.4 Nest Survival

The best-approximating nest survival (DSR; daily survival rate) model from Chapter 2 included standardized nest initiation date (IDATE, $IDATE^2$) as a continuous variable, habitat type, pintail pair density (PINDEN) and the proportion cropland (PCTCROP). Because nests are not modeled individually when applying this model, I assign the population of initiated nests by thirds into early, mid, and late nest categories and assign the median IDATE value from each third of the nest population used in the analysis. I use model estimating equations from Chapter 2 (Appendix C) to generate daily survival rates (DSR) for each habitat type in early, mid, and late seasonal periods given landscape-specific covariate inputs.

4.2.2.5 Nesting Effort and Hatching Success

I estimate the population of nests generated by a population of females by setting the breeding propensity and renesting propensity of females and setting the maximum number of nests initiations attempted. The number of first nest initiations ($Init_1$) by seasonal nesting period is defined by the equation:

$$Init_{1,j} = N * p_{nest} * q_{ij},\ j = 1, 2, \ldots, J \quad (4.1)$$

where N denotes the population of nesting females, p_{nest} denotes the proportion of females that initiate at least one nest (i.e., breeding propensity), and q_{ij} denotes the proportion of the females that initiate their *i*th nest in the *j*th seasonal period (early, mid, or late), given that females initiate at least *i* nests ($\sum_j q_{ij} = 1$). Because breeding propensity has not been estimated for pintails, I used the average propensity (0.90) observed for radio-marked mallards (*Anas platyrhynchos*) studied in the Canadian PPR (Devries et al. 2008b). The proportion of females nesting in early, mid, and late periods was set at 0.36, 0.33, and 0.310, respectively, to attain a generally equal nest initiation distribution among seasonal periods after accounting for female mortality and nest survival effects on nest production (see below).

Subsequent nest initiations (i.e., renests; $i = 2, 3$) by seasonal period are defined by the equations:

$$Init_{i,1} = Init_{i-1,1} * (1 - NS_1) * r_1 * q_{i1} \quad (4.2)$$

$$Init_{i,2} = \left[Init_{i-1,1} * (1 - NS_1) * r_1 * q_{i2}\right] + \left[Init_{i-1,2} * (1 - NS_2) * r_2 * \left(\frac{q_{i2}}{q_{i2} + q_{i3}}\right)\right] \quad (4.3)$$

$$Init_{i,3} = \left[Init_{i-1,1} * (1 - NS_1) * r_1 * q_{i3}\right] + \left[Init_{i-1,2} * (1 - NS_2) * r_2 * \left(\frac{q_{i3}}{q_{i2} + q_{i3}}\right)\right] + \left[Init_{i-1,3} * (1 - NS_3) * r_3\right] \quad (4.4)$$

where NS_j denotes the weighted average nest survival (i.e., DSR[32]; daily nest survival over the 32-day laying and incubation period of pintails; Klett etal.1986) over habitats during the *j*th seasonal period, and r_j denotes the probability that an unsuccessful female initiates a renest in the *j*th seasonal period. I set a declining renest probability of 0.85, 0.5, and 0.2 for early, mid, and late seasonal periods, respectively, based on the pattern of seasonally declining renest probability observed for mallards (Arnold et al. 2010). I allowed only *i* = 3 nest initiation attempts on the basis of pintail renesting behaviour reported by Grand and Flint (1996a) and Guyn and Clark (2000). Finally, to account for the effect of female mortality through the nesting season on nest production, I multiplied the sum of estimated nest initiations in each seasonal period by an estimate of the proportion of females that survive to the midpoint of each seasonal period (0.967, 0.865, and 0.780, respectively, using Devries et al.'s [2003] results for mallards).

The sum of nests initiated by surviving females within each seasonal period above ($Nests_j$), are subsequently distributed among habitats within a seasonal period based on the equation:

$$Nests_{hj} = \left(\frac{P_{hj} * A_h}{\sum_h^k P_{hj} * A_h}\right) * Nests_j \quad (4.5)$$

where $Nests_{hj}$ denotes the number of nests initiated in habitat *h* in the *j*th seasonal period, P_{hj} denotes the relative preference for habitat *h* in the *j*th seasonal period (Appendix C), and A_h

denotes the proportional availability of habitat *h* (constant for a given site among seasonal periods).

Hence, hatched nests in each habitat and seasonal period are provided by the equation:

$$Hatched_{hj} = Nests_{hj} * NS_{hj} \quad (4.6)$$

where NS_{hj} represents nest survival rate for each habitat and seasonal period (Appendix C).

4.2.3 Combining the Models

Because nest survival and habitat selection models (Chapter2) were derived at a study area scale representing approximately 41 km^2, model application should occur at a similar scale. Thus, as a demonstration of model application, I extracted the long-term estimated average pintail pair population for constituent 41 km^2 grid blocks for the 'Boundary Plateau' PHJV Target Landscape in southern Saskatchewan. Habitat availability in each grid block was estimated by converting AAFC and USGS land cover categories into model habitat categories making some data-based assumptions about land uses (e.g., percent of grass in pasture; Appendix D). The productivity model was run individually on constituent grid blocks and the results summed to estimate the number of hatched nests from the target landscape. I further demonstrate the use of the model to estimate the influence of habitat change on pintail productivity by converting 10% of existing spring-seeded cropland to alternate habitats (idle grass or winter wheat).

4.3 Results

4.3.1 Models of Pintail Distribution

I examined 11 models relating 1961–2009 average pintail pair count to covariates associated with MWBPHS survey transects within the PPR of North America (Table 4.2). The best-approximating model included 1) quadratic effects of wetland area and wetland count each interacting with country on the linear term, 2) quadratic effects of latitude and longitude with an interaction between their linear terms, 3) interactions between the linear effects of latitude and longitude with wetland area and count, respectively, 4) a quadratic effect of the amount of cropland in the landscape interacting in the linear term with wetland count and latitude, and finally, 5) a linear topographic effect of elevation variation including an interaction with wetland count (Table 4.3).

Pintails showed similar nonlinear asymptotic responses to wetland area and wetland count in Canada and the U.S. although the response to wetland count was more linear in the U.S. than in Canada (Figure 4.3a,b). Pintail abundance generally peaked at mid-latitude and mid-longitude (i.e., southern Saskatchewan) although peak abundance in the eastern portion of the PPR was centered near the border of North and South Dakota (Figure 4.3c). Latitude had a strong effect on pintail abundance relative to the amount of cropland in the surrounding landscape. At lower latitudes, typical of the U.S. PPR, pintail abundance was negatively related to the amount of cropland in the landscape, whereas pintails were positively related to the amount of cropland at latitudes centered in the Canadian PPR (Figure 4.3d). Finally, pintails settled at higher abundance in landscapes with low topographic variation (Figure 4.3e). Model fit as measured by Spearman's correlation between observed and predicted counts was 0.82. The median difference

between observed and predicted breeding pintails pairs at the transect segment level was -0.6 (range: -27.7–30.8).

Applying the best-approximating model in ArcMap to data surfaces representing covariate values at the modeled scale revealed substantial spatial variation in pintail pair density across the PPR (estimated pairs/km^2; Figure 4.4). As a model check, I compared the sum of pixel estimates within survey strata boundaries in ArcMap (Figure 4.4) to the strata average pintail population counted in the MWBPHS survey during 1961–2009 (Table 4.4). To convert pair estimates to population estimates, I multiplied the map estimates by 2 (to account for pairs) and added 12% (to account for the average number of estimated non-breeders counted during surveys (J. Devries, unpublished data). The relationship between strata-based map estimates and MWBPHS counts was strong (Figure 4.5; $r^2 = 0.97$) and the regression coefficient indicated minimal bias ($\beta = 1.07 \pm 0.05$). However, over and under-estimation were evident in some strata (Table 4.4).

4.3.2 Models of Pintail Productivity

When pintail population and wetland area (in km^2) were set to their median values (thus providing the PINDEN covariate), and habitat availability was set to its average over observed study sites (thus providing PCTCROP and PCTGRASS covariates), the model of pintail productivity estimated average nest survival of 12%, and hen success (i.e., proportion of females hatching ≥ 1 egg) of 15.5%. At average habitat availability on study sites used to generate nest site preference and nest survival, the majority of nests were located in grazed grasslands and spring-seeded cropland (35 and 33%, respectively) where nest survival was relatively low to moderate (~7–12%).

Given the interaction of pintail breeding density and landscape composition on both habitat preference and nest survival, however, relative habitat use and productivity can vary

substantially depending on the landscape context of the breeding site. For example, when pintail density is varied from low to high at a site with average habitat composition, the proportion of nests in grassland (grazed and idle) declines from ~60% to ~17%, and use of spring-seeded cropland increases from ~17% to ~68% (Figure 4.6b). Consequently, hen success varied from ~26% at low pintail density to ~3% at high pintail density in this landscape (Figure 4.7). Similarly, landscape composition (i.e., habitat availability) varying from cropland-dominated to grassland-dominated decreased use of cropland and increased use of grassland (Figure 4.6a-c), but increases in hen success were only realized at lower pintail densities (Figure 4.7).

When the models were used together to estimate pintail production from the Boundary Plateau PHJV Target Landscape in southern Saskatchewan (Figure 4.8), production was very low. While supporting an estimated 14,732 pintail pairs on average, only 1,029 of an estimated 19,658 initiated nests survived to hatch (Table 4.5). Converting 10% of spring-seeded cropland to idle grass and winter wheat increased the estimated production to 1,099 and 1,492 hatched nests, respectively (Table 4.5). Low production from this landscape is attributed to a high percentage of the landscape being spring-seeded cropland (mean: 55%; Figure 4.8) and a high proportion of nests being initiated in spring-seeded cropland (65%) where nest survival was low.

4.4 Discussion

For migratory species like waterfowl that have broad geographic distribution, decisions about where to settle and breed, at multiple scales, can have important demographic consequences. Spatial variation in habitat selection and reproductive success within the breeding range of North American ducks is evident at the continental scale (e.g., Smith 1970, Hestbeck 1995), between cropland versus grassland-dominated landscapes in the PPR (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), and at local scales among specific available

nesting habitats (e.g., Klett et al. 1988, Chapter 2). Understanding and modeling these patterns of habitat selection, and their potential influence on reproductive success, is a first step in linking habitat (and habitat change) to population demography (Pulliam 1988, Dunning et al. 1995). Models that capture this linkage can provide useful tools for habitat conservation planning at local and regional scales, and aid in understanding the combined effects of population management efforts through habitat conservation and harvest management as occurs for many species of North American waterfowl (Anderson et al. 2007, Mattsson et al. 2012).

The pintail distribution model described here is the first to estimate the long-term average distribution of pintails across the entire PPR, although modeling efforts have occurred separately for several duck species in the U.S. and Canadian portions of the PPR. Reynolds et al. (1996) used only wetland basin-specific waterfowl counts to model the relationship between wetland size and class and species abundance, and applied these relationships to U.S. National Wetland Inventory maps to estimate waterfowl density across the U.S. PPR. Using an approach similar to my approach, Ducks Unlimited Canada has modeled the abundance of seven duck species combined across the Canadian PPR using waterfowl counts and associated wetland and upland covariates along MWBPHS survey segments. Despite these efforts, seamless models of duck distribution across the entire PPR have been hampered, until recently, by availability of spatial covariate datasets spanning the entire region (e.g., wetland inventory), and conservation planning efforts limited by political boundaries (but see Doherty et al., in press). The pintail distribution model presented here is the first of its type for the PPR using spatial covariate databases available for the entire region, and similar model development for other dabbling duck species should be straightforward.

The general relationships between pintail pair abundance and wetland and upland covariates observed in my distribution model are similar to those observed in Chapter 3, with the addition of several interactions among covariates. Differences between predicted pintail abundance relative to wetland area and count between Canada and the U.S. may simply reflect the different sources of data, although Miller and Duncan (1999), using pintail and pond counts gathered across the PPR as part of the MWBPHS, also report that pintail abundance per wetland was higher in Canada than the U.S. Models also indicate pintail abundance shows strong nonlinear geographical trends with latitude and longitude such that peak abundance was generally centered in southern Saskatchewan, a pattern noted by previous authors (e.g., Bellrose 1980), and in previous analyses of these data (Johnson and Grier 1988, Podruzny et al. 2002). Importantly, this modeling effort includes an interaction between latitude and land use such that pintails tend to settle at greater abundance in landscapes with more cropland at higher latitudes, and in landscapes with less cropland at lower latitudes (Figure 4.3d). This pattern likely reflects differences in the juxtaposition of croplands and wetlands between the Canadian and U.S. PPR rather than a geographic difference in behaviour. A consequence of this pattern is that pintails may be more susceptible to cropland nesting, and therefore lower recruitment, in years when they settle disproportionally in the Canadian PPR. Latitude of settling within the PPR did not appear as a factor affecting recruitment in my Chapter 3 analysis, however. Finally, the overall negative association of pintails with topographic variation quantifies the previously described habit of pintails to associate with landscapes containing shallow, less persistent wetlands as are characteristic of flatter topography (Hochbaum and Bossenmeier 1972, Stewart and Kantrud 1973, Austin and Miller 1995).

The map of long-term average pintail pair distribution developed here provides habitat managers with a useful tool for targeting habitat conservation efforts to regions where they may benefit the most pintails over the long term. Furthermore, maps of relative species density across broad regions allow planning and prioritization of effort to occur at a similar scale. This is an important criterion for cost-efficiency of conservation efforts given that techniques for protection and restoration of duck production in agricultural landscapes is often intensive, requiring considerable money and manpower. Thus, in conjunction with other sources of information (e.g., land cover and use), knowledge of relative species distribution can provide conservation planners with an objective means of prioritizing geography for appropriate conservation actions. Finally, a very useful feature of model-based maps generated in ArcGIS is that they facilitate extraction of estimated population size at user-defined scales for use in associated planning and population models.

While understanding spatial variation in abundance is valuable to guide where habitat conservation efforts may have the greatest impact, being able to link population distribution with habitat-specific demographic models is critical in predicting potential population responses to management efforts (Pulliam 1988). Previous research has established nest survival as a key vital rate affecting population growth rate of waterfowl (Cowardin and Johnson 1979, Hoekman et al. 2002), and hence, much waterfowl management effort has been expended on habitat conservation and management efforts affecting this vital rate (Williams et al 1999).

The mechanistic model of pintail productivity I have developed here is an attempt to capture the primary habitat-related influences on nest survival for pintails in the PPR. Mechanistic models of waterfowl productivity have been previously developed for the mallard (Mallard Model: Johnson et al. 1987) and pintail (Flint et al. 1998; hereafter, the Flint model), however,

only the Mallard Model incorporates habitat-specific nest site preference and nest survival thereby making it more suitable as a habitat management and conservation planning tool. Both models are stochastic, individual-based models unlike the deterministic population cohort model structure I have described here. I have avoided a stochastic model because I incorporate parameter estimates from sources outside the data I used in constructing the habitat preference and nest survival models (e.g., mallard renesting propensity, breeding season survival). Regardless, my model structure includes the primary biological components and nest habitat linkages that field data indicate affect pintail production to the point of hatch in the PPR. Future refinements could incorporate stochasticity and pintail vital rates into this model structure as suitable data become available.

Other than the difference in model type and inclusion of habitat-specific vital rates, there are several differences between my pintail productivity model and the Flint model that warrant comparison. The Flint model was developed using data collected from pintails breeding on Alaska's Yukon-Kuskokwim Delta (YKD) and therefore is likely not applicable to the PPR. For example, YKD nest survival estimates average 25%, much higher than observed in most PPR nesting studies (e.g., Klett et al. 1988, Greenwood et al. 1995, Ch. 2). Furthermore, the Flint model includes clutch size and duckling survival to fledge. My model ignores clutch size and only estimates production to the point of hatched nests, the current endpoint of most PPR habitat management efforts. Critically, my model also includes breeding pair density and landscape-level habitat interactions on nest habitat preference and nest survival based on analyses conducted in Chapter 2. These density and habitat effects produce the highest nest survival in landscapes with low pintail density and low amounts of cropland, both factors that vary spatially and should be considered in habitat conservation and management activity. The strong negative

influence of duckling survival on pintail recruitment observed in Alaska by Flint et al. (1998) argues strongly for the inclusion of this vital rate in my PPR model, especially if duckling survival can be linked to upland and wetland habitat characteristics amenable to management. Existing information suggests that pintail duckling survival in the PPR is generally higher than in Alaska (Grand and Flint 1996b, Guyn and Clark 1999).

Collectively, the models of pintail distribution and productivity provide valuable insights regarding the interaction between species distribution, habitat availability, and potential demographic consequences. For example, while spring-seeded cropland has low nest survival and was not a preferred habitat, a substantial proportion of pintail nests may be initiated in spring-seeded croplands where high pintail breeding density and high amounts of croplands co-occur. This was demonstrated in the example of the Boundary Plateau PHJV Target Landscape, where the highest densities of breeding pintails occur in landscapes (41 km^2 grid blocks) comprised almost entirely of cropland (Figure 4.8b). The resulting 7% hen success was lower than that observed in Alaska (Flint et al. 1998). A similar phenomenon was noted in Greenwood et al.'s (1995) study where 45% of pintail nests were found in cropland despite cropland only being intermediate in terms of relative preference among the habitats examined.

The models of pintail distribution and productivity developed here make several assumptions that may limit their use. First, the model of pintail distribution represents the average distribution of pintails from 1961–2009. Annual pintail distribution can vary dramatically in response to widespread prairie drought and regional variation in moisture, and total population size can vary over time (Johnson and Grier 1988, Miller et al. 2003). An underlying assumption is that pintail responses to covariates has not changed over time and thus in the absence of dramatic landscape change, the current model accurately reflects the long-term

average relative distribution of pintails across the PPR. Further, I used land cover data *circa* 2000–2001 as a covariate to represent landscape conditions with the assumption that these relatively recent conditions represent long-term characterization of land use. I justify this given that, while land use has changed somewhat during 1961–2009, cropland and grassland amounts at regional scales has changed relatively little during this period (J. Devries, unpublished data).

The productivity model developed here, and much of the waterfowl conservation effort in the PPR, assumes that nest survival is the primary vital rate affecting pintail population growth rate. This assumption has been tested and confirmed for prairie-nesting mallards (Hoekman et al. 2002, Howerter et al. 2014); however, empirical information suggests that breeding vital rates for pintails may differ from mallards (e.g., lower nest and duckling survival, lower renesting propensity; Klett et al. 1988, Greenwood et al. 1995, Peterson 1999, Guyn and Clark 1999, 2000). A sensitivity analysis of existing pintail vital rate data is warranted to examine this assumption.

The productivity model further assumes that the habitat preference and nest survival models apply across the PPR despite being developed primarily from field data gathered in Canada. Although methods and habitat definitions among studies differ (e.g., previous studies did not systematically search cropland), relative habitat-specific nest survival and preference rates are comparable to those reported by Greenwood et al. (1995) for the Canadian PPR and by Klett et al. (1988) for the U.S. PPR, with the exception of their most preferred habitats, "Brush" and "Planted cover", respectively. "Brush" is defined as patches of low shrub growing in native pasture, and would be included in my Grazed Grassland category; "Planted cover" is seeded grass-legume mixtures left idle, and would be included in my Idle Grassland category. Planted

cover was present at few of the study sites used in developing my productivity model but sample sizes were too small to warrant a separate habitat definition.

In summary, the comprehensive approach to modelling developed here represents the first to estimate habitat selection of pintails at local and region-wide scales within the PPR and quantify the potential reproductive consequences of these behavioural patterns. While often discussed in theory, empirically-based, spatially explicit demographic models on this scale are rare for animals (Saracco et al. 2010, Folmer et al. 2014). The models developed here provide 1) tools to estimate the impact of alternative habitat conservation and management efforts on pintail productivity in different landscape contexts, 2) tools to estimate the impact of background landscape/land use changes on pintail productivity (e.g., agricultural policy change), and 3) a mechanism to link the impact of habitat change and habitat management across the primary breeding range of the pintail to population demographic response. The development of similar models for other dabbling ducks in the Prairie Pothole Region is warranted to improve our understanding of the effects of habitat management on populations of these economically important species.

Table 4.1. Description of habitat types included in the Pintail Productivity Model (PPM) for the Prairie Pothole Region. Habitats are based on analysis of nest habitat preference and nest survival in Chapter 2, with the addition of 'Other' and 'Trees' which are assigned a preference of 0 in the PPM. Other and Trees are included here because they will commonly comprise a component of the habitat composition extracted from areas of interest in the PPR when applying this model.

Habitat type	**Description**
Spring cropland	Areas that are tilled and planted to grain or row crops in the spring, or that retain previous year's crop stubble and are fallowed (tillage or chemical) during the growing season.
Fall cropland	Croplands that are seeded and germinate in the fall, go dormant over the winter, and grow to maturity the following spring and summer (primarily winter wheat and fall rye).
Grassland - idle	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs ≤ 30%) and have not been disturbed by haying, mowing, or grazing.
Grassland - grazed	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs ≤ 30%) that have been primarily disturbed by grazing (may contain some hayed or mowed lands but exclude lands specifically planted for hay-see Hayland).
Hayland	Areas that have been seeded to grass and/or legume mixtures for forage production and that are cut for hay annually.
Wetland	All areas, regardless of size, mapped as wetland according to definitions in Cowardin et al. (1979). Wetlands may be undisturbed, grazed or hayed.
Other	Areas typically considered non-habitat such as road surfaces, unvegetated gravel pits, developed urban areas.
Trees	Areas with woody plants (trees or tall shrubs) 6-m or greater in height and having an aerial cover ≥ 30%. Trees may be idle or grazed.

Table 4.2. Eleven ranked models that relate the long-term average number of pintail pairs counted on May Waterfowl Breeding Population and Habitat Survey (MWBPHS) survey segments, 1961–2009, with wetland, land use, landform, and geographic covariates[a] across the Prairie Pothole Region. Models are ranked by ΔAIC_c; the best-approximating model (in **bold**) was used to map pintail distribution across the PPR in ArcGIS. The NULL model included parameter estimates for the intercept and dispersion only. For each model, I present -2*log-likelihood (-2LL), the number of parameters in the model (*k*), Akaike's Information Criterion adjusted for small sample size (AIC_c), the difference in AIC_c between each model and the top-ranked model (ΔAIC_c), and the model weight (*w*).

MODEL	-2LL	*k*	AICc	ΔAICc	*w*
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM*WETCNT	**4823.9**	**22**	**4869.2**	**0.0**	**0.337**
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM^2 + CVSRTM*WETCNT	4822.3	23	4869.7	0.5	0.262
WETHA2 + WETCNT2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT2 + LAT*WETHA + LONG2 + LONG*WETHA + LONG*WETCNT + LAT*LONG + CROP2 + CROP*WETCNT +CROP*LAT + CVSRTM^2 + CVSRTM*WETCNT	4821.5	24	4871	1.8	0.137
WETHA^2 + WETCNT^2 + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM*WETCNT	4827.9	21	4871.1	1.9	0.130
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETHA + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM^2 + CVSRTM*WETHA + CVSRTM*WETCNT	4821.1	25	4872.7	3.5	0.058
WETHA^2 + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM*WETCNT	4832.4	20	4873.5	4.3	0.039
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LAT*WETCNT + LONG^2 + LONG*WETHA + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETCNT +CROP*LAT + CVSRTM^2 + CVSRTM*WETHA + CVSRTM*WETCNT	4820.7	26	4874.5	5.3	0.024
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LAT*WETCNT + LONG^2 + LONG*WETHA + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETHA + CROP*WETCNT +CROP*LAT + CVSRTM^2 + CVSRTM*WETHA + CVSRTM*WETCNT	4820.5	27	4876.5	7.3	0.009
WETHA^2 + WETCNT^2 + COUNTRY*WETHA + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LAT*WETCNT + LONG^2 + LONG*WETHA + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*WETHA + CROP*WETCNT +CROP*LAT + CROP*LONG + CVSRTM^2 + CVSRTM*WETHA + CVSRTM*WETCNT	4820.5	28	4878.6	9.4	0.003
WETHA^2 + COUNTRY*WETCNT + LAT^2 + LAT*WETHA + LONG^2 + LONG*WETCNT + LAT*LONG + CROP^2 + CROP*LAT + CVSRTM*WETCNT	4841.8	19	4880.7	11.5	0.001
NULL	5924.2	2	5928.2	1059.0	0.000

[a] Covariate definitions: WETHA – estimated wetland area (ha) within May Waterfowl Breeding Population and Habitat Survey segment boundaries (hereafter, 'survey segment'), WETCNT – estimated wetland basin count within survey segment boundaries, COUNTRY – country in which the survey segment is located (United States or Canada), LAT – latitude of the survey segment centroid, LONG – longitude of the survey segment centroid, CROP – percent of the survey segment defined as cropland by digital land cover datasets, CVSRTM – coefficient of variation in 90 m pixel elevations within survey segment boundaries.

Table 4.3. Best-approximating model parameter estimates (β) and standard errors (SE) for covariates predicting the long-term average number of pintail pairs counted within 11.6 km^2 areas along May Waterfowl Breeding Population and Habitat Survey (MWBPHS) segments in the Prairie Pothole Region, 1961–2009. See Table 2 for acronym definitions.

Parameter	β	**SE**
Intercept	-129.21	10.37
WETHA	2.507	0.72
$WETHA^2$	-0.0377	0.0103
WETCNT	-0.4493	0.3995
$WETCNT^2$	-0.0149	0.0068
$COUNTRY_{CAN}$	1.402	0.231
$COUNTRY_{CAN}$*WETHA	-0.1247	0.0624
$COUNTRY_{CAN}$*WETCNT	-0.1764	0.0349
LAT	13.63	2.50
LAT^2	-4.834	0.444
LAT*WETHA	-0.393	0.150
LONG	17.50	1.83
$LONG^2$	-1.537	0.102
LONG*WETCNT	0.121	0.036
LONG*LAT	3.135	0.360
CROP	-12.02	1.570
$CROP^2$	-0.897	0.233
CROP*WETCNT	-0.173	0.052
CROP*LAT	2.781	0.323
CVSRTM	-0.599	0.083
CVSRTM*WETCNT	0.077	0.023

Table 4.4. Comparison of May Waterfowl Breeding Population and Habitat Survey (MWBPHS) stratum-specific 1961–2009 average pintail population estimates versus cumulative model-based pixel estimates in ArcGIS. To convert ArcGIS pair estimates to total population estimates, summed pixel-based estimates were multiplied by 2 (to convert from pairs to individuals) and inflated by 12% (to account for the average number of estimated non-breeders counted during surveys).

MWBPHS Stratum	MWBPHS 1961–2009 Average Pintail Breeding Population	ArcMap Estimate of Average Pintail Breeding Population	Difference (ArcMap-MWBPHS estimate)	Percent Difference
26	200,538	201,421	883	0.4
27	132,804	123,507	-9,298	-7.0
28	155,185	134,625	-20,560	-13.2
29	136,540	113,530	-23,010	-16.9
30	118,810	129,534	10,724	9.0
32	439,438	409,159	-30,278	-6.9
33	100,065	124,409	24,344	24.3
34	85,633	112,039	26,406	30.8
35	88,504	90,089	1,585	1.8
38	8,551	11,577	3,026	35.4
39	33,334	38,003	4,669	14.0
40	23,432	20,202	-3,230	-13.8
41	128,041	91,391	-36,650	-28.6
45	190,113	178,482	-11,631	-6.1
46	96,002	84,467	-11,535	-12.0
47	6,400	11,112	4,712	73.6
48	138,629	136,503	-2,126	-1.5
TOTAL	2,082,021	2,010,052	-71,969	-3.5

Table 4.5. Estimated pintail pairs extracted from 41 km^2 grids comprising the Prairie Habitat Joint Venture (PHJV) Boundary Plateau Target Landscape in southwestern Saskatchewan, and Pintail Productivity Model estimates of total initiated nests, and hatched nests, at base landscape composition, and with 10% of spring-seeded cropland converted to idle grassland and winter wheat.

Landscape Condition	Estimated Pintail Pairs	Total Initiated Nests	Total Hatched Nests
Base Landscape Composition[1]	14,732	19,659	1,029
Converting 10% of Spring-seeded Cropland to Idle Grass	14,732	19,620	1,099
Converting 10% of Spring-seeded Cropland to Winter Wheat	14,732	19,472	1,492

[1] Base landscape composition: 55.4% spring-seeded cropland, 33.1% grazed grassland, 4.0% idle grassland, 3.8% hayland, 1.5% trees, 1.2% wetland, 1.1% other, and 0% fall-seeded cropland.

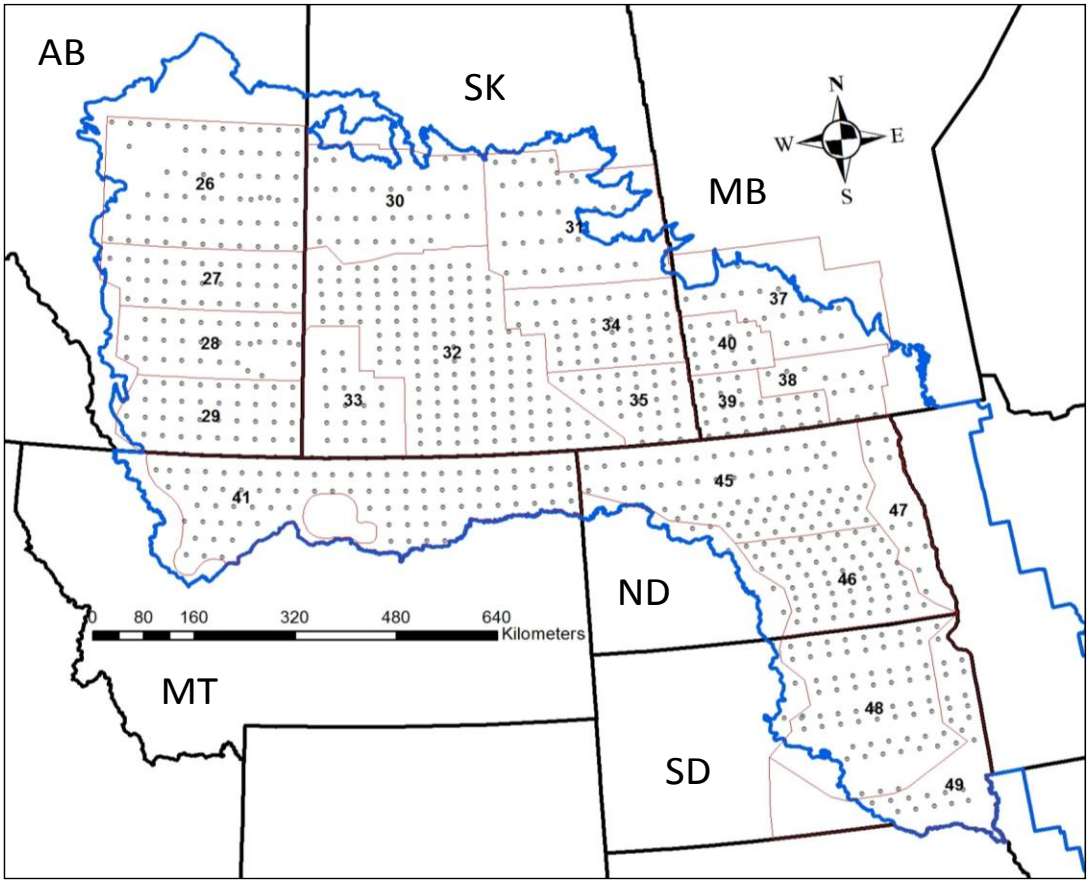

Figure 4.1. Extent and location of 809 May Waterfowl Breeding Population and Habitat Survey (MWBPHS) transect segments (dots represent centroids of segments) and strata (numbered polygons) within the Prairie Pothole Region (outlined in blue) of Canada and the United States.

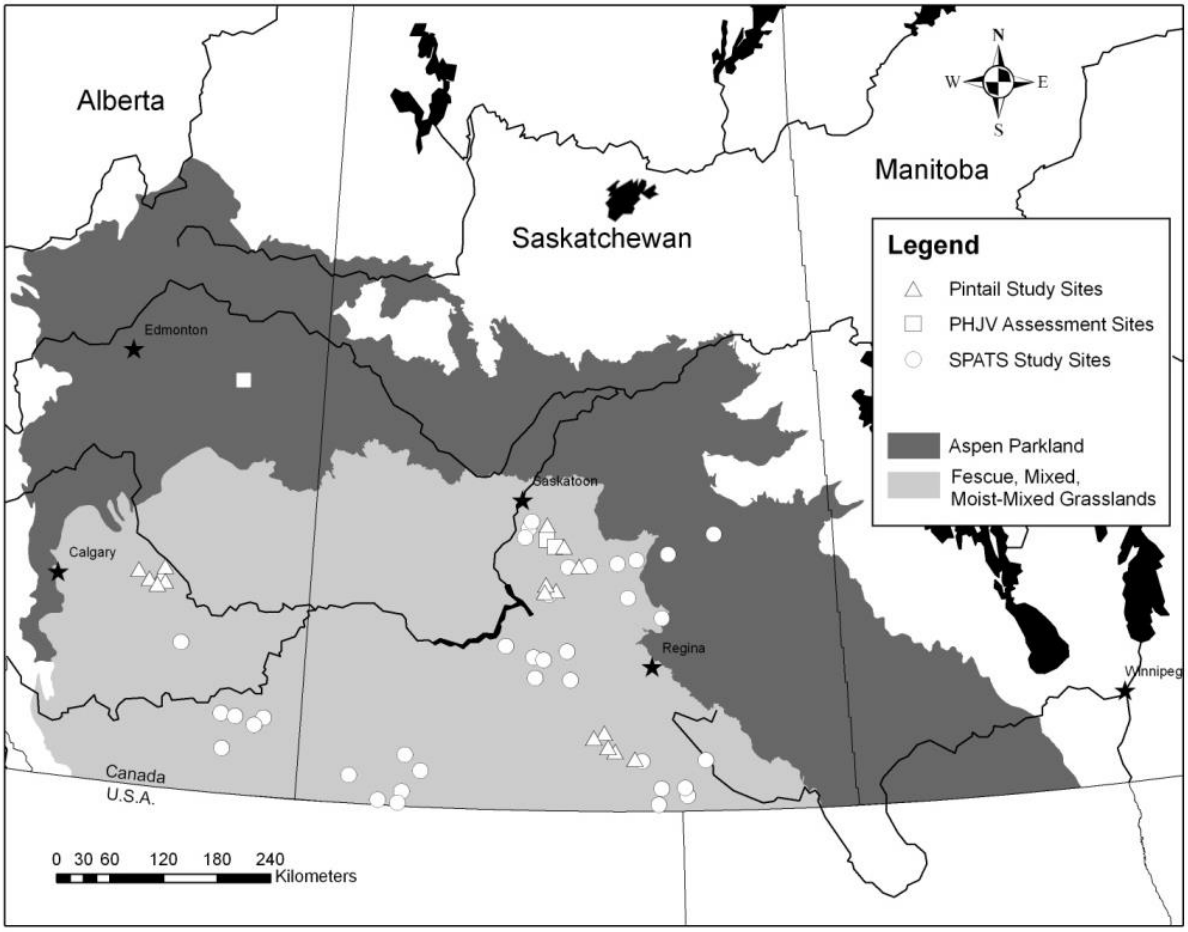

Figure 4.2. Location of Ducks Unlimited Canada waterfowl nesting study areas within Grassland and Aspen Parkland Ecozones of prairie Canada, 1993–2011, from which pintail nesting data was used to estimate nest habitat preference and nest survival rates.

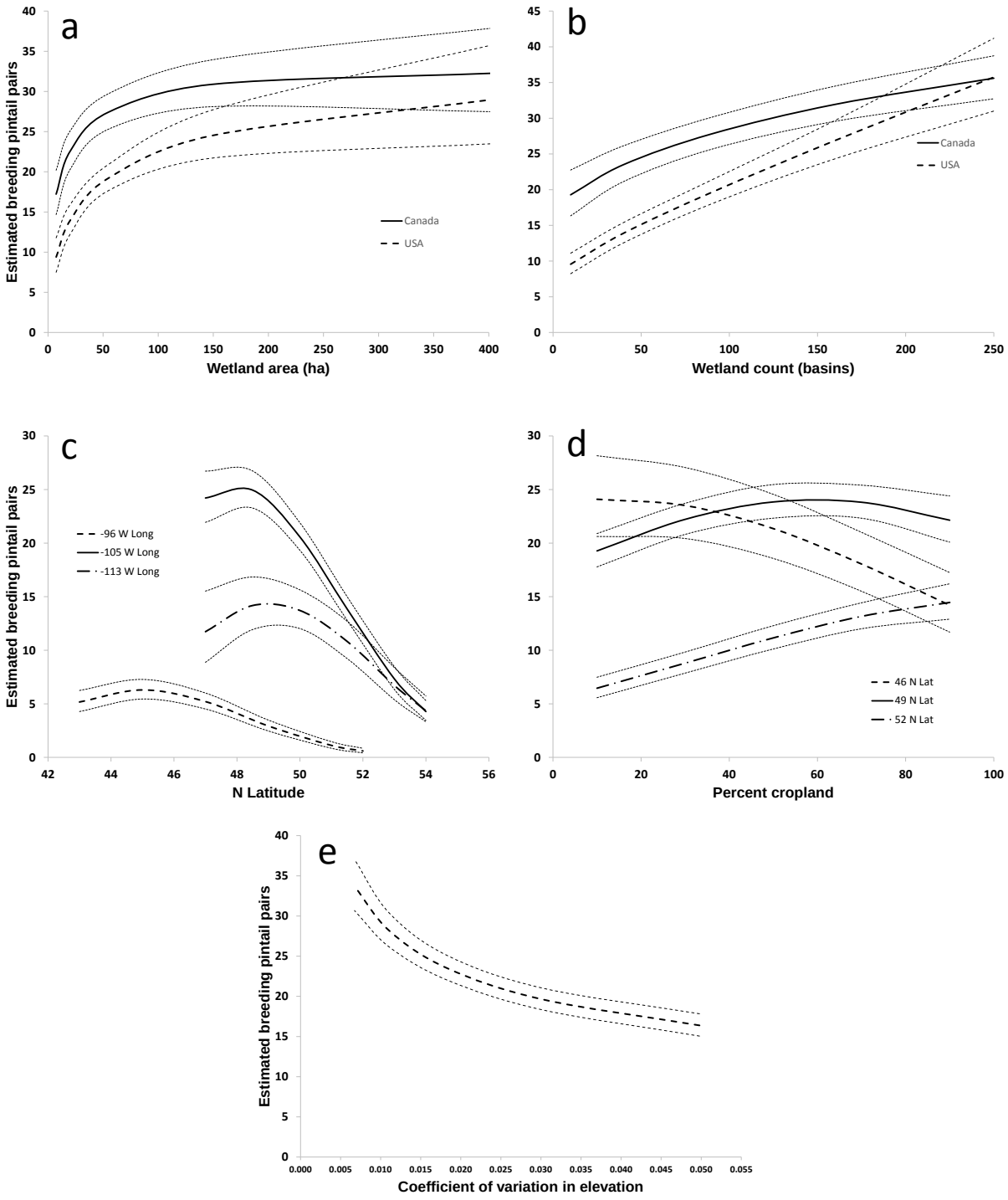

Figure 4.3. Best-approximating model estimates of long-term average (1961–2009) breeding pintail pairs counted within May Waterfowl Breeding Population and Habitat Survey (MWBPHS) segment boundaries relative to a) wetland area and b) wetland count in Canada and the United States, c) latitude and longitude, d) percent cropland, and e) coefficient of variation in Shuttle Radar Topography Mission (CVSRTM) elevations within the Prairie Pothole Region.

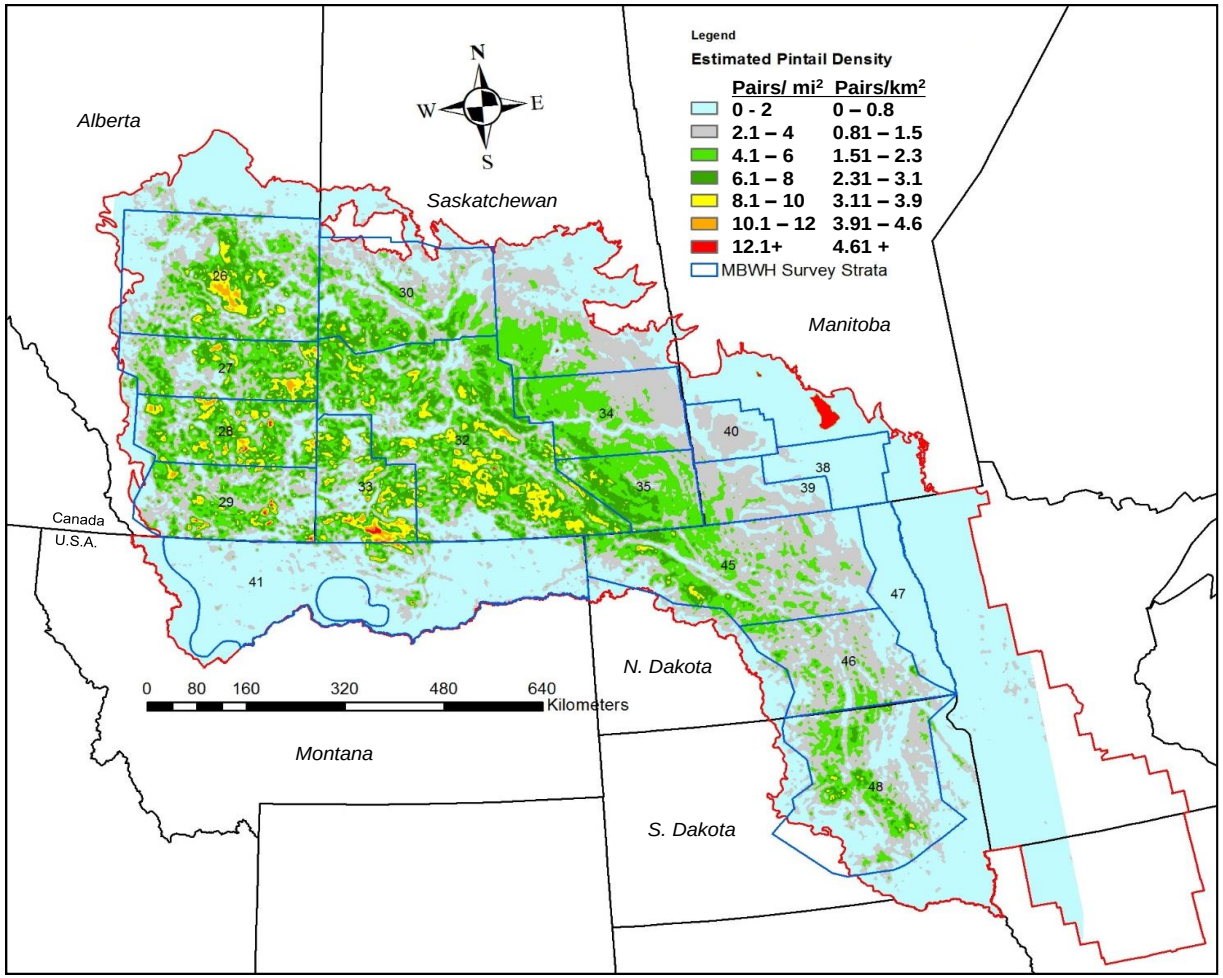

Figure 4.4. Best-approximating model-based estimates of long-term average (1961–2009) breeding pintail pair density (pairs/mi^2, pairs/km^2) as a function of wetland, upland, and geographic covariates in the Prairie Pothole Region (PPR) of North America. This map was generated in ArcGIS by applying the best-approximating model equation to spatial data layers coding individual covariate values. Map-based estimates of pintail population extracted in ArcGIS were checked against long-term average population estimates reported by the USFWS within the May Waterfowl Breeding Population and Habitat Survey (MWBPHS) strata outlined in blue (and also correspond with areas and numbers shown in Figure 4.1). Note: pintail pair density here represents the number of pintail pairs within a geographic unit [km^2] of space rather than a km^2 of wetland as used for the pintail density [PINDEN] covariate in previous chapters).

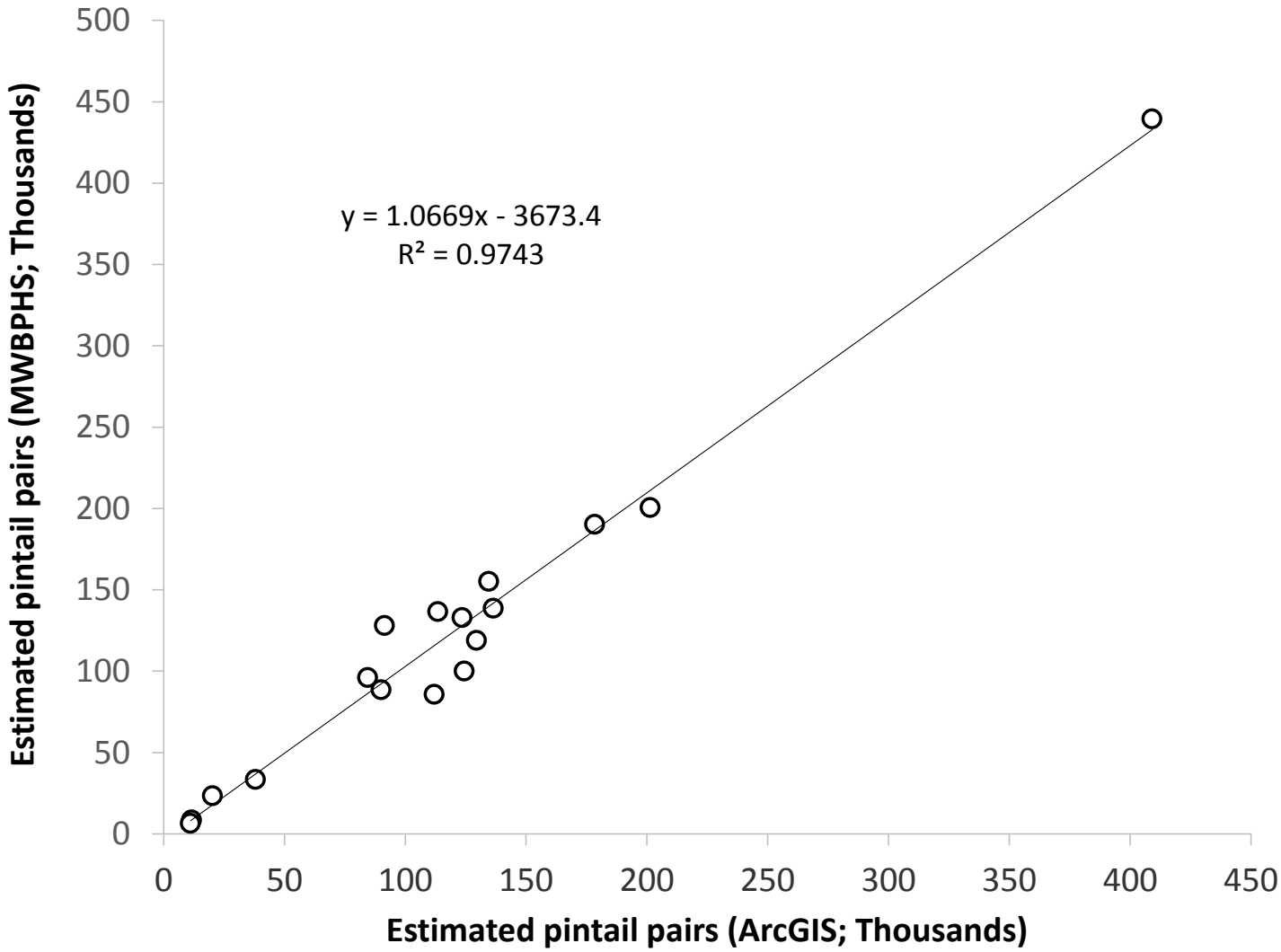

Figure 4.5. Relationship between the May Waterfowl Breeding Population and Habitat Survey (MWBPHS) long-term average (1961–2009) strata-level estimates of breeding pintail pairs and ArcGIS extracted estimates of pintail breeding pairs within MWBPHS strata boundaries (see Figure 4.4) covering the Prairie Pothole Region (PPR) of North America.

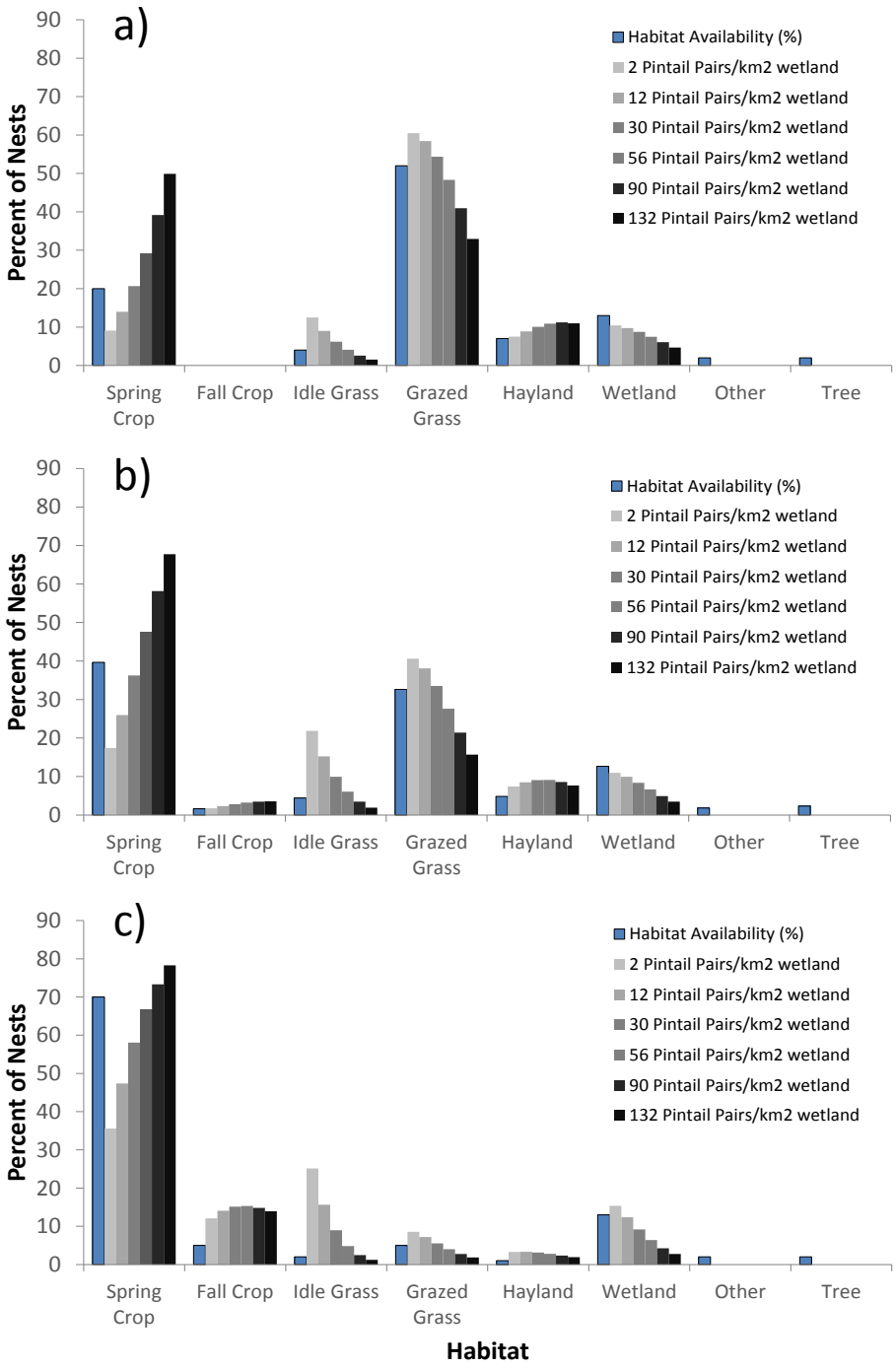

Figure 4.6. Plots of predicted nest distributions among available habitats, derived from the Pintail Productivity Model and showing the influence of pintail population density (2–132 pintail pairs/km^2 wetland) and landscape habitat composition as landscape habitat availability varies from grassland-dominated to cropland-dominated. Landscape habitat availabilities shown are a) 20% cropland, b) 42% cropland, and c) 75% cropland. Percent habitat availability is shown in blue bars while the percent of nests in each habitat is shown as shades of gray corresponding to specific breeding pair densities.

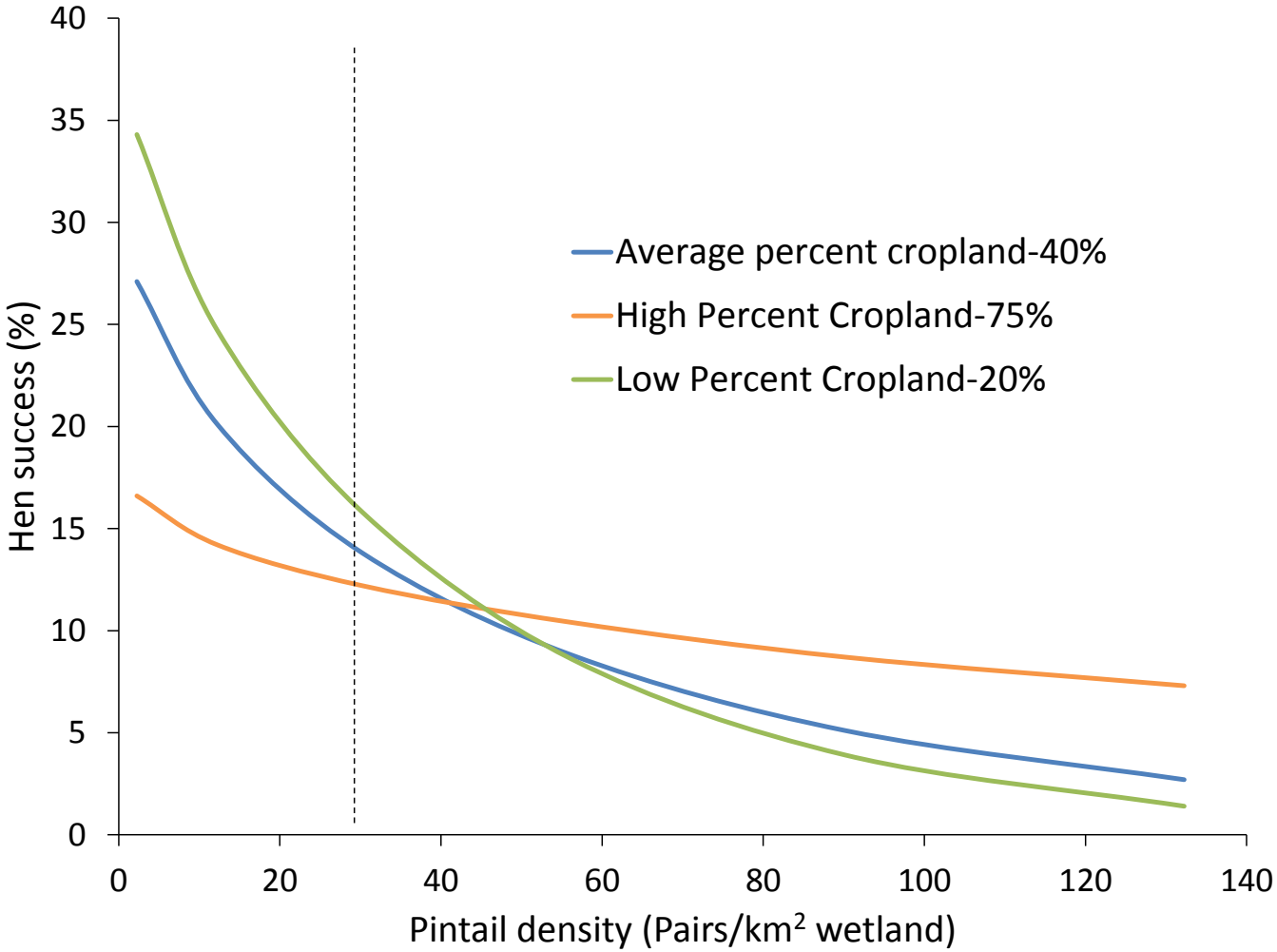

Figure 4.7 Plot of predicted hen success estimates as pintail population density (pairs/km^2 wetland) varies in landscapes composed of low (20%), average (40%), and high (75%) amounts of cropland in the surrounding landscape (41 km^2). Average percent cropland (40%) represents the average observed among nesting study sites used to develop the Pintail Productivity Model and not necessarily the average landscape composition in the PPR. The vertical dashed line represents the average pintail density observed among study sites used to develop the productivity model (see Figure 4.2).

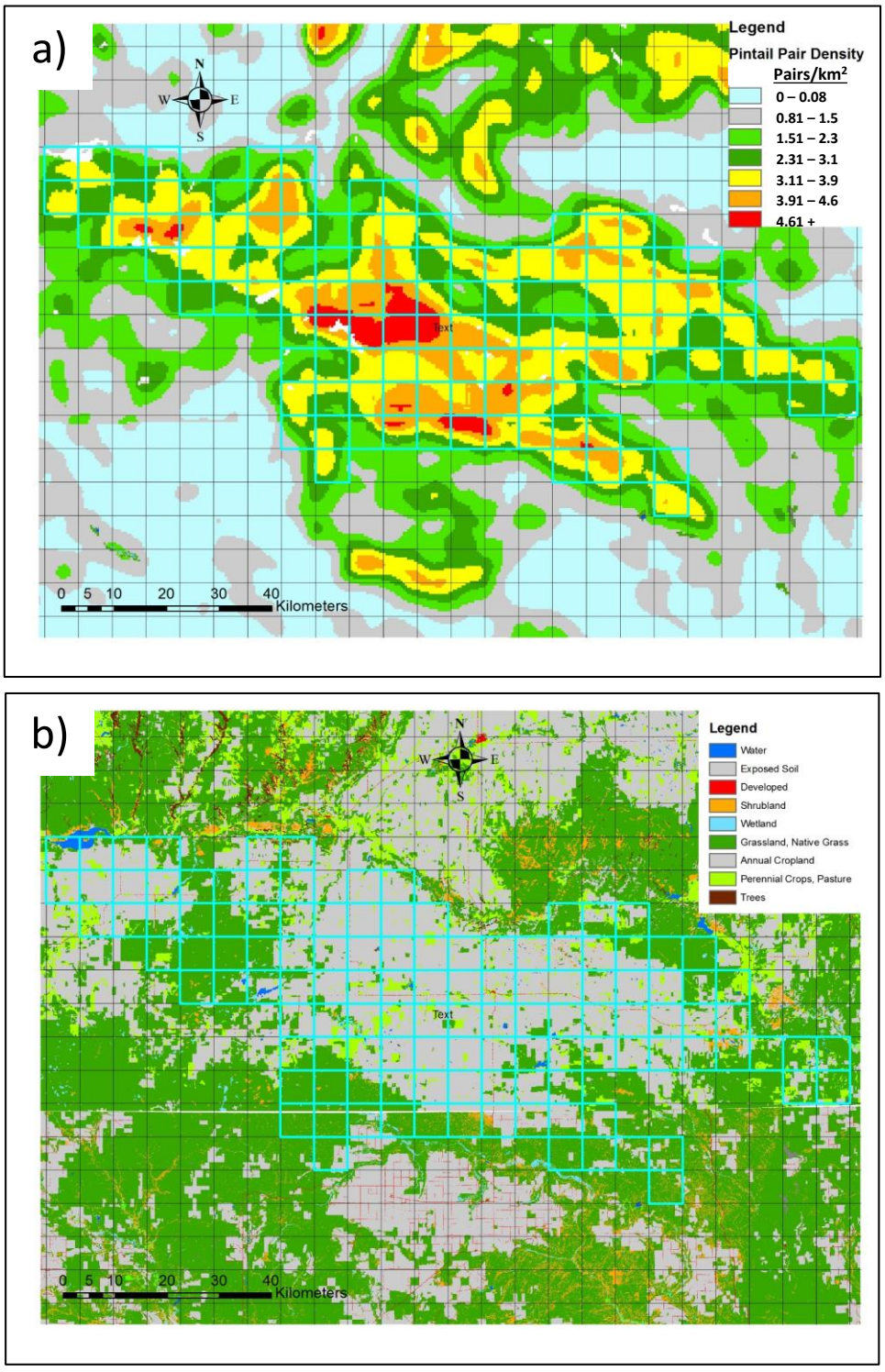

Figure 4.8 Example of 41 km^2 grids (outlined in blue) comprising the Boundary Plateau Prairie Habitat Joint Venture Target Landscape overlying, a) estimated pintail breeding pair density, and b) Agriculture and Agri-food Canada (AAFC) land cover map of south-western Saskatchewan.

CHAPTER 5. SYNTHESIS

Understanding the nature of species interactions with their environment, and consequent effects on population dynamics, underpin the fields of population ecology and conservation biology. The dynamic interaction between habitat selection, reproductive success, and survival, at multiple scales, are some of the most fascinating aspects of these fields; important not only for understanding habitat-mediated demographic processes that sustain populations, but for insights into evolutionary processes as well. Consequently, a rich body of theory has developed to explain the patterns and processes observed across taxa.

An overarching goal of this dissertation has been to address both the theoretical and applied aspects of habitat selection in a migratory bird, the northern pintail. Accordingly, I have focused on two broad, yet related, objectives; 1) to test for correspondence between habitat selection and components of fitness, in accordance with evolutionary theory, at multiple scales, and 2) to construct predictive models incorporating habitat preference and reproductive success to estimate pintail abundance, distribution, and productivity in response to changing habitat conditions; information that is fundamental to conservation planning and population modeling. I review my general findings below and where applicable, suggest further studies to address unresolved questions.

Fretwell and Lucas (1969), among others, provided a landmark theoretical framework under which habitat selection may be adaptive; where individuals achieve the best fitness outcomes possible given available options. Similar adaptive mechanisms of habitat selection include the density-dependent buffer effect postulated by Brown (1969), and the functional response of Mysterud and Ims (1998), where habitat use is subject to trade-offs in response to the

availability of a dominant habitat. The potential for mal-adaptive habitat selection mechanisms to arise also is recognized; where poor habitats are selected (Schlaepfer et al. 2002), or good habitats are avoided (Gilroy and Sutherland 2007, Patten and Kelly 2010). Across theories, the important influence of scale in habitat selection decisions has also been advocated (e.g., Chalfoun and Martin 2007).

I provide evidence that pintails select nesting habitats adaptively, although not consistently, and with important modifying influences. In general, nest habitat patches and landscapes that confer the best available nest survival and recruitment potential receive higher use, but relationships were modified by population density and landscape context. Based on empirical data on nest survival among habitat patches within landscapes, habitat types with low nest survival (e.g., wetlands) were avoided, whereas habitat that provided greater nest survival (e.g., idle grass, hayland) were selected, especially later in the nesting season. Spring-seeded cropland, with poor nest survival, was used as available until late in the nesting season when it was avoided. While not meeting the definition of an ecological trap, *per se*, the overwhelming availability of spring-seeded cropland in much of the pintail's prairie breeding range ensures many pintail nests are subject to low nest survival in this habitat. Fall-seeded cropland (typically winter wheat) provided the starkest example of within-season change in selection; avoided early but preferred late in the nesting season. Similar to the findings of Duebbert and Kantrud (1987) and Devries et al. (2008a), winter wheat had the highest nest survival of any habitat. Thus, winter wheat may represent a perceptual trap for early nesting pintails (Patten and Kelly 2010).

Anecdotally, the observed patterns of habitat use among habitats follow changes in vegetation height and concealment value which generally improve through the nesting season. Vegetation in winter wheat and haylands typically increased in height and concealment the most,

whereas idle grasslands maintained good concealment value for duck nests through the nesting season. Increasing correspondence between selection and nest survival among habitats through the nesting season suggests vegetation height and/or thickness may provide the proximate cue upon which selection is based.

In addition, I provide evidence that population density and landscape composition interactively affected nest survival and habitat selection in ways that reduced, but did not disrupt, adaptive habitat selection. At high pintail density, nest survival declined and pintails shifted selection from higher nest survival habitat (idle grassland) to lower nest survival habitat (spring-seeded cropland) such that habitats were generally used as available at high density (while still experiencing differential survival among habitats). This pattern most closely fits predictions under the Brown (1969) buffer effect version of the ideal-dominance hypothesis, accounting for population density effects on preference among habitats; suboptimal habitats are used at high population density but not necessarily through territorial mechanisms. A similar effect was observed in habitat use by red-winged blackbirds where increasing population density led to greater increase in the use of less suitable habitats (Clark and Weatherhead 1987). This phenomenon undoubtedly disperses pintail nests more widely across the landscape at higher population density, however, I hesitate to comment on the adaptive significance of this without knowledge of similar patterns in conspecifics. The adaptive value of clustering versus dispersing nests in terms of nest predation risk remains unclear (Larivière and Messier 1998, Ackermann et al. 2004, Ringelman et al. 2012, 2013). The use of agent-based models (Ringelman 2014), in conjunction with models of nest habitat selection and nest survival probability as presented in Chapter 4 (including conspecifics), may hold promise as a means of examining various hypotheses about density-dependent predation in PPR landscapes.

An alternate hypothesis may be that when population density suppresses the absolute fitness differences among habitats, the relative benefits of selecting among habitats disappears. For example, a 1% versus 2% fitness differential between habitats may be below a threshold that triggers strong choices, whereas at 10% versus 20%, the benefits of such choices become substantial. Experimental examination of this hypothesis, and potential mechanisms involved, is warranted in a system where predation rates among habitats can be manipulated (e.g., Gotceitas and Colgan 1989).

Decreasing nest survival with the amount of cropland in a landscape is a previously established phenomenon in nesting ducks (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), likely resulting from attendant differences in the community composition and foraging efficiency of predators (Sargeant et al. 1993, Sovada et al. 2000, Phillips et al. 2003, DUC unpublished data). However, few studies have examined or reported changes in habitat selection with landscape context in birds (e.g., Donovan et al. 1997). In my study, preference among habitats changed markedly depending on whether grassland or cropland were dominant land covers on the study area. In cropland-dominated landscapes; habitats with high nest survival were selected or used as available, while habitats with lower nest survival were all avoided. In grassland-dominated landscapes, all habitats were generally used as available. This is an example of a functional response in habitat use as proposed by Mysterud and Ims (1998), where habitat preference changes in response to the availability of a main habitat type. That relative nest survival among habitats did not vary with percent cropland in my analysis suggests that the mechanisms responsible for among habitat differences in nest survival are stable, and the observed pattern in use was not in response to changing nest survival among habitats. Greater correspondence between preference and nest survival in cropland-dominated landscapes may be

a direct response to an increase in predation pressure in these landscapes as noted above (e.g., Spaans et al. 1998, Forstmeier and Weiss 2004, but see Pöysä et al. 2001). Martin (1995) suggested that the nest predation – nest site relationship is likely too unpredictable to favor phenotypic plasticity in nest site selection. However, Forstmeier and Weiss (2004) suggest that when one main predator has a large effect on reproductive success, adaptive assessment is more likely. In landscapes dominated by cropland, the red fox (*Vulpes vulpes*) is often the dominant predator of both duck nests and attendant females (Sargeant et al. 1984, 1993, Sovada et al. 2000), thus placing enormous selective pressure on selection of safe nest sites. High amounts of cropland (or low amounts of contiguous grassland) may be a cue to shift nest sites into habitats with greater concealment such as those preferred here. Further experimental examination of how habitat selection and predation rates may vary under changing habitat availability is a much needed area of research.

At a larger scale, representing pintail selection among landscapes within the PPR, adaptive associations of pintails with the landscape characteristics that are known or suspected of being correlated with greater recruitment were mixed. But, when pintails settled to a greater extent in landscapes that were wetter than normal, contained more grassland, and were moderate in elevation variation (a measure of local topography), the population-level measure of recruitment (juvenile to adult ratio in the fall harvest) was higher.

For PPR waterfowl in general, population responses to varying wetland conditions is well known; ducks are typically more abundant in wetter years and locations (Johnson and Grier 1988, Bethke and Nudds 1995). The PPR is characterized by frequent wet-dry cycles that affect the number and inundation level of isolated pothole wetlands (Euliss et al. 2004, Johnson et al. 2004), and pintails in particular are known for their nomadic nature; settling to breed in regions

of the PPR that are newly wet (Hochbaum and Bossenmeier 1972, Johnson and Grier 1988, Austin and Miller 1995).

The drawdown and rewetting of prairie pothole wetlands during this cycle drives the very high abundance and productivity of aquatic invertebrates in these wetland systems, especially during the rewetting phase (Murkin 1989, Walker et al. 2013). Accordingly, areas that are wetter than normal should provide more food for breeding females (Batt et al. 1989, Krapu et al. 1997), are typified by increased breeding propensity and renesting effort of resident ducks (Krapu et al. 1983, Eldridge and Krapu 1988), increased nest survival (Walker et al. 2013, Howerter et al. 2014), and improve survival of ducklings (Rotella and Ratti 1992, Cox et al. 1998, Krapu et al. 2006). Thus, wetter-than-average landscapes likely signal abundant food resources, early and prolonged breeding opportunities, and successful recruitment of young. As predicted, my analysis showed that pintails exhibited a strong positive association with landscapes that were wetter than average.

As noted above, and confirmed for pintails in Chapter 2, landscapes containing more grassland and less cropland have the potential for greater nest survival, a primary component of recruitment in prairie-breeding ducks (Hoekman et al. 2002). My analysis of pintail annual distribution relative to grassland within the PPR indicates that this effect can roll-up to a population effect, producing greater juvenile to adult ratios in the fall harvest when pintail distribution shows more overlap with grassland (and less overlap with cropland). The habitat composition of the surrounding landscape also is likely a readily assessed cue for pintails when deciding where to settle and breed, and thus, an adaptive selection hypothesis would predict greater use of landscapes with more grassland and less cropland. However, my analysis indicated pintail distribution within the PPR was unrelated to the amount of cropland in a

landscape when PPR populations were low but was positively associated with cropland when populations were high. This pattern reflects the buffer effect proposed by Brown (1969) where increases in population size are reflected by a greater increase in use of poor-quality sites, and reduced productivity. Gill et al. (2001) nicely demonstrated this effect at the population level with wintering black-tailed godwit (*Limosa limosa islandica*) use of estuaries in Britain; use of lower quality estuaries increased the greatest as population size increased, resulting in lower rates of population increase. Among studies that have examined theoretical models of habitat selection, most provide support for an ideal-dominance model (reviewed in Petit and Petit 1996). For pintails, the observed effect may also be a maladaptive response to a historically adaptive preference for seasonal wetlands that predominate in landscapes that are currently under intensive agricultural production. If so, this may be an example of an ecological trap operating at a scale larger than immediate nest habitat availability – the previously adaptive cue, landscapes containing flooded seasonal wetlands, has been altered by change in land use and anthropogenic nest site disturbance (Schlaepfer et al. 2002).

I included local variation in elevation in my examination of pintail landscape selection given anecdotal observations that pintails are more prone than other ducks to occupy landscapes with low topographic relief (i.e., flatter; Hochbaum and Bossenmeier 1972, Stewart and Kantrud 1974). This was likely a response to the predominance of shallow temporary and seasonal wetlands that characterize these landscapes in wet years (Stewart and Kantrud 1973, 1974). In contrast to my prediction, pintail recruitment indices were lower in years when the population was associated to a greater degree with flatter landscapes within the PPR. As with cropland landscapes above, the association depended on PPR population size such that changes in population size were most reflected in greater use of flatter landscapes. Again, this was

consistent with the buffer effect of Brown (1969), but also with a population moderated ecological trap, if use of flatter landscapes is driven by availability of seasonal wetlands that are now associated with altered landscapes.

While my results have indicated important density-dependent mechanisms are at play for pintails selecting both nest habitats and landscapes from those available, the density-dependent mechanisms are not obvious. Pintails, unlike some dabbling duck species, are not territorial in the traditional sense; adopting a mate-defense strategy over more traditional defense of resources within a territory (Smith 1968, McKinney 1965). However, pintails, more than other ducks, are known for their prolonged and energetic pursuit flights often ending with attempted rape of the female, and occurring most frequently during the nesting period (McKinney 1965, Smith 1968, Titman and Seymour 1981). It is thus plausible that female harassment is more common at higher population density, with consequent impacts on reproductive success. McKinney (1965) and Smith (1968) suggest that this behaviour may disperse nesting females, although evidence for this is lacking (Duncan 1987). Derrickson (1978) noted that choice of wetlands by female pintails, and hence access to preferred wetland habitats, may be influenced by male sexual harassment. In mallards, abnormally high breeding densities led to increased strife among pairs, frequent rape of females, and high frequency of nest abandonment (Titman and Lowther 1975). Nest abandonment was unrelated to population density in my study (J. Devries, unpublished data) so alternate mechanisms are more likely.

It seems unlikely that pintail nest density alone would cue increased predation by nest predators (e.g., Larivière and Messier 1998) although my data suggested this may occur when all duck nests are considered. It is plausible that increased competition among females for food, and frequent harassment by males, at high densities, could reduce nest attendance leading to

increased discovery of nests by predators, but support for this is tenuous (Derrickson 1978, Drever et al. 2004). Kowalchuk (2013) observed selection of grassland-dominated landscapes by older female pintails suggesting age and experience may improve adaptive selection in this species. It is plausible also that harassment of yearling females by males may be greater than older females leading to displacement from optimal breeding landscapes. Regardless, further examination and experimental tests of density-dependent mechanisms operating at both the level of the nest and landscape selection are needed. Close observation of individually marked wild female pintails, including monitoring of pair behaviour and behaviour at the nest site, under varying breeding densities and landscape contexts, may help to shed light on potential mechanisms involved.

While examination of adaptive habitat selection is of great interest from a theoretical standpoint, the linkage between selection of habitat and demographic consequences is applied in the field of conservation biology (Caughley 1994). Caughley (1994) advocated for a theoretical understanding of habitat-demographic relationships as a basis for conservation actions to address population declines in species of concern. While pintails currently are not close to extinction, recent declines in their population, particularly the segment that has historically settled in prairie Canada, is suggestive that some aspect of the habitat-demographic relationship has changed. Potential explanations have included increasing cropland as an ecological trap (Miller and Duncan 1999), changing land use (Podruzny et al. 2002), and declines in annual survival (Miller et al. 2003), but conclusive data remain elusive.

Recent analyses of pintail survival demonstrate that annual survival rates for males or females have not changed substantially since the 1970s (Rice et al. 2010), lending little support to the declining survival hypothesis. My analysis of breeding landscape associations, nest

habitat preference, and nest survival together provide tools to explore the potential impact of these factors across the PPR. Pintail habitat preference generally does not suggest that spring-seeded cropland is an ecological trap; rather croplands are used as available. But croplands are a dominant habitat in many areas where pintails choose to settle, especially at high population density. Thus, a large percentage of nests are exposed to low nest survival across the PPR where croplands, on average, comprise approximately 50% of the landscape (J. Devries, unpublished data). If we assume that nest survival was somewhat higher in summerfallow (as it was undisturbed through the early nesting season), and consider that summerfallow comprised 30–50% of annually tilled land at its peak in the 1970's (Carlyle 1997), a demographic impact of declining summerfallow across the Canadian PPR seems plausible (Podruzny et al. 2002). The models I have developed in Chapter 4 will allow these types of retrospective and forecasting scenarios to be examined further, given spatial and temporal data on changing land use practices such as that available from the federal Censuses of Agriculture, or via land use forecasting efforts (e.g., Radeloff et al. 2012).

Importantly, the models I developed in Chapter 4 provide the ability to derive empirically-based estimates of the impact of conservation actions. For example, my analysis suggests that exposure of nests to low nest survival in spring-seeded cropland may be limiting recruitment of pintails. Considering that opportunities to change the inherent distribution of pintails within the PPR are likely limited, conservation actions should be targeted to improve nest survival through conversion of spring-seeded cropland to winter wheat, haylands (especially where hay cutting occurs later in the season), idle grass, or pasture in landscapes that attract, on average, moderate densities of pintails. The ability to employ this type of empirical biologically-based modeling over such a large geographic expanse is an important advance in conservation

planning for North American waterfowl, with exciting and useful implications for linking habitat change to pintail demography.

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APPENDIX A

All nest survival models examined at nest, patch, landscape, and multi-scale levels. Models in **bold** represent full models at each scale.

Scale/Model	k	QAIC	Δ QAIC
Nest Level			
DISTWET IDATE IDATE^2	5	1700.1	0.00
IDATE IDATE^2	4	1701.2	1.11
NESTAGE DISTWET IDATE IDATE^2	6	1701.2	1.12
NESTAGE DISTWET IDATE IDATE^2 IDATE*DISTWET	7	1702	1.83
NESTAGE DISTWET IDATE IDATE^2 IDATE*DISTWET IDATE^2*DISTWET	**8**	**1703.3**	**3.16**
NULL	2	1703.3	3.21
NESTAGE DISTEDG IDATE IDATE^2 IDATE*DISTEDG IDATE^2*DISTEDG	8	1704.4	4.28
IDATE	3	1704.8	4.71
Patch Level			
HAB	7	1530.8	0.00
HAB PATCHSZ HAB*PATCHSZ	**13**	**1531.5**	**0.69**
HAB PATCHSZ	9	1532.2	1.39
NULL	2	1542.7	11.91
Nest + Patch Level			
IDATE IDATE^2 HAB HAB*IDATE	14	1440.4	0.00
IDATE IDATE^2 HAB	9	1441.3	0.90
DISTWET IDATE IDATE^2 HAB HAB*IDATE	15	1441.3	0.91
DISTWET IDATE IDATE^2 HAB HAB*DISTWET HAB*IDATE	20	1443.6	3.14
HAB	7	1444.4	3.95
IDATE HAB	8	1446.2	5.81
DISTWET IDATE IDATE^2 HAB HAB*DISTWET HAB*IDATE HAB*IDATE^2	**25**	**1451.1**	**10.72**
NULL	2	1455.0	14.62
Landscape Level			
PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 PCTCROP*PINDEN	9	1641.8	0.00
PINDEN DUCKDEN DUCKDEN^2 WEDGDEN WEDGDEN^2	7	1642.4	0.58
PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 PCTCROP*PINDEN PCTCROP*DUCKDEN	10	1643.7	1.86
PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2	8	1643.8	2.00
PINDEN DUCKDEN DUCKDEN^2 PCTGRASS WEDGDEN WEDGDEN^2	8	1643.9	2.09
PINDEN	3	1643.9	2.10
PINDEN DUCKDEN DUCKDEN^2	5	1644.4	2.61
PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 PCTCROP*PINDEN PCTCROP*DUCKDEN PCTCROP*DUCKDEN^2	**11**	**1644.6**	**2.80**
PINDEN DUCKDEN DUCKDEN^2 WEDGDEN	6	1644.9	3.07
PINDEN DUCKDEN DUCKDEN^2 PCTGRASS WEDGDEN WEDGDEN^2 PCTGRASS*DUCKDEN PCTGRASS*DUCKDEN^2	10	1645.2	3.42
PINDEN DUCKDEN	4	1645.9	4.05
PINDEN DUCKDEN DUCKDEN^2 PCTGRASS WEDGDEN WEDGDEN^2 PCTGRASS*DUCKDEN	9	1645.9	4.06
PINDEN DUCKDEN DUCKDEN^2 PCTGRASS WEDGDEN WEDGDEN^2 PCTGRASS*PINDEN PCTGRASS*DUCKDEN PCTGRASS*DUCKDEN^2	**11**	**1647.2**	**5.40**
NULL	2	1652.1	10.28

Multi-scale			
IDATE IDATE^2 HAB PINDEN	10	1365.4	0.0
IDATE IDATE^2 HAB PINDEN DUCKDEN DUCKDEN^2 PCTCROP PCTCROP*PINDEN	14	1366.6	1.2
IDATE IDATE^2 HAB PINDEN PCTCROP PCTCROP*PINDEN	12	1366.9	1.5
IDATE IDATE^2 HAB HAB*IDATE PINDEN DUCKDEN DUCKDEN^2 PCTCROP PCTCROP*PINDEN	19	1366.9	1.5
IDATE IDATE^2 HAB PINDEN PCTCROP	11	1367.3	1.9
IDATE IDATE^2 HAB PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 PCTCROP*PINDEN	16	1367.4	1.9
IDATE IDATE^2 HAB PINDEN DUCKDEN DUCKDEN^2	12	1367.6	2.2
IDATE IDATE^2 HAB HAB*IDATE PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 PCTCROP*PINDEN	21	1368.0	2.6
IDATE IDATE^2 HAB	9	1369.4	4.0
IDATE IDATE^2 HAB PINDEN PCTCROP DUCKDEN DUCKDEN^2 PCTCROP*DUCKDEN PCTCROP*DUCKDEN^2	15	1370.3	4.9
HAB	7	1372.5	7.0
IDATE IDATE^2 HAB HAB*IDATE PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 HAB*PINDEN PCTCROP*PINDEN	26	1376.1	10.7
IDATE IDATE^2 HAB HAB*IDATE PINDEN DUCKDEN DUCKDEN^2 PCTCROP WEDGDEN WEDGDEN^2 HAB*PINDEN PCTCROP*PINDEN HAB*PCTCROP	**31**	**1382.1**	**16.7**
NULL	2	1383.4	18.0

APPENDIX B

Full models used to identify the best model combination of alternate variables explaining variation in pintail habitat selection ratios. Categorical habitat (HAB) and habitat-specific daily nest survival rate (HAB_DSR) model suites include habitat interactions with covariates identified in competing multi-scale nest survival models. Variables examined include two IDATE categorical definitions (IDAT3CAT: early, mid, late; IDAT2CAT: mid, other), pintail pair density (PINDEN), non-pintail duck density (DUCKDEN), and landscape percent cropland (PCTCROP) and grassland (PCTGRASS). Models containing interactions include their constituent main effects. Models highlighted in **bold** (lowest AIC) were taken forward for model reduction.

MODEL	Parameters	AIC
HAB SUITE		
HAB*IDAT3CAT + HAB*PINDEN + HAB*DUCKDEN + HAB*PCTCROP	37	6089.0
HAB*IDAT3CAT + HAB*PINDEN + HAB*DUCKDEN + HAB*PCTGRASS	**37**	**6089.0**
HAB*IDAT2CAT + HAB*PINDEN + HAB*DUCKDEN + HAB*PCTCROP	31	6115.5
HAB*IDAT2CAT + HAB*PINDEN + HAB*DUCKDEN + HAB*PCTGRASS	31	6115.5
HAB_DSR SUITE		
HAB_DSR*IDAT3CAT + HAB_DSR*PINDEN + HAB_DSR*DUCKDEN + HAB_DSR*PCTCROP	13	6134.4
HAB_DSR*IDAT3CAT + HAB_DSR*PINDEN + HAB_DSR*DUCKDEN + HAB_DSR*PCTGRASS	**13**	**6131.2**
HAB_DSR*IDAT2CAT + HAB_DSR*PINDEN + HAB_DSR*DUCKDEN + HAB_DSR*PCTCROP	11	6138.0
HAB_DSR*IDAT2CAT + HAB_DSR*PINDEN + HAB_DSR*DUCKDEN + HAB_DSR*PCTGRASS	11	6134.9

APPENDIX C

Nest habitat preference (selection ratio) and daily nest survival rate estimating equations by seasonal period (early, mid-season, late) from the best-approximating models examined in Chapter 2.

MODELS OF HABITAT SELECTION RATIO

Early Nests

Spring Crop Selection Ratio
=EXP(-5.1842 + -1.2925 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.3181 + 0.2511*PINDEN + 0.005521*PCTGRASS)
Fall Crop Selection Ratio
=EXP(-5.1842 + 0.2878 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + -0.3597 + 0.184*PINDEN+ -0.01596*PCTGRASS)
Idle Grass Selection Ratio
=EXP(-5.1842 + 2.495 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.5432 + -0.1297*PINDEN+ -0.01772*PCTGRASS)
Grazed Grass Selection Ratio
=EXP(-5.1842 + 0.008915 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.893 + 0.0193*PINDEN+ 0.001129*PCTGRASS)
Hayland Selection Ratio
=EXP(-5.1842 + 0.9036 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.05644 + 0.1183*PINDEN+ -0.01337*PCTGRASS)
Wetland Selection Ratio
=EXP(-5.1842 + 0 + -0.4721 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0+ 0)
Other Selection Ratio = 0
Tree Selection Ratio = 0

Mid-season Nests

Spring Crop Selection Ratio
=EXP(-5.1842 + -1.2925 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0.2511*PINDEN + 0.005521*PCTGRASS)
Fall Crop Selection Ratio
=EXP(-5.1842 + 0.2878 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0.184*PINDEN+ -0.01596*PCTGRASS)
Idle Grass Selection Ratio
=EXP(-5.1842 + 2.495 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + -0.1297*PINDEN+ -0.01772*PCTGRASS)
Grazed Grass Selection Ratio
=EXP(-5.1842 + 0.008915 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0.0193*PINDEN+ 0.001129*PCTGRASS)
Hayland Selection Ratio
=EXP(-5.1842 + 0.9036 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0.1183*PINDEN+ -0.01337*PCTGRASS)
Wetland Selection Ratio
=EXP(-5.1842 + 0 + 0 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0+ 0)
Other Selection Ratio = 0
Tree Selection Ratio = 0

Late Nests

Spring Crop Selection Ratio

=EXP(-5.1842 + -1.2925 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + -0.2372 + 0.2511*PINDEN + 0.005521*PCTGRASS)

Fall Crop Selection Ratio

=EXP(-5.1842 + 0.2878 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.769 + 0.184*PINDEN+ -0.01596*PCTGRASS)

Idle Grass Selection Ratio

=EXP(-5.1842 + 2.495 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.08361 + -0.1297*PINDEN+ -0.01772*PCTGRASS)

Grazed Grass Selection Ratio

=EXP(-5.1842 + 0.008915 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + -0.03272 + 0.0193*PINDEN+ 0.001129*PCTGRASS)

Hayland Selection Ratio

=EXP(-5.1842 + 0.9036 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0.08791 + 0.1183*PINDEN+ -0.01337*PCTGRASS)

Wetland Selection Ratio

=EXP(-5.1842 + 0 + -0.05339 + 0.0771*PINDEN + 0.01152*PCTGRASS + 0 + 0+ 0)

Other Selection Ratio = 0

Tree Selection Ratio = 0

MODELS OF DAILY NEST SURVIVAL RATE (DSR)

Early Nests (IDATE = -2.3050)

Spring Crop DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Fall Crop DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Idle Grass DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Grazed Grass DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Hayland DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Wetland DSR

=EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-2.3050 + -0.116*-2.3050^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Mid-season Nests (IDATE = -0.5250)

Spring Crop DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Fall Crop DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Idle Grass DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Grazed Grass DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Hayland DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Wetland DSR
=EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282*-0.525 + -0.116*-0.525^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

Late Nests (IDATE = 0.9446)
Spring Crop DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Fall Crop DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.8953 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Idle Grass DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.5518 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Grazed Grass DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.231 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Hayland DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*0.4676 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))
Wetland DSR
=EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP) / (1+(EXP(3.6735 + -0.1282* 0.9446 + -0.116* 0.9446^2 + 1*-0.2396 + -0.1741*PINDEN + -0.01423*PCTCROP + 0.00192*PINDEN*PCTCROP)))

APPENDIX D

Method used to convert Agriculture and Agri-Food Canada (AAFC) and U.S. Geological Survey (USGS) land cover categories to Pintail Productivity Model habitat categories for 41 km^2 grid blocks covering the Prairie Pothole Region (PPR). The proportion of each land cover class identified below occurring in each grid block was summarized into Pintail Productivity Model habitat classes from each source as follows:

AAFC Land Cover

Productivity Model Habitat	**Land Cover Class**
Spring Cropland	Annual Cropland
Fall Cropland (set as 0)	-
Grassland – idle[a]	12% of Grassland, Native Grass
Grassland – grazed[a,b]	88% of Grassland, Native Grass + 50% of Perennial Crops, Pasture
Hayland[b]	50% of Perennial Crops, Pasture
Wetland	Water + Wetland
Other	Exposed Soil + Developed
Trees	Coniferous + Deciduous + Mixed Forest + Shrubland

USGS Land Cover

Productivity Model Habitat	**Land Cover Class**
Spring Cropland	Cultivated Crops
Fall Cropland (set as 0)	-
Grassland - idle[a]	12% of Grassland / Herbaceous
Grassland - grazed[a,b]	88% of Grassland / Herbaceous + 50% of Pasture / Hay
Hayland[b]	50% of Pasture / Hay
Wetland	Open Water + Emergent Herbaceous Wetlands + Woody Wetlands
Other	All 'Developed' categories + Barren Land
Trees	Evergreen Forest + Deciduous Forest + Mixed Forest + Shrub / Scrub

[a] I estimated the 12% idle : 88% grazed ratio based on the observed ratio of idle : grazed grassland on waterfowl nesting study areas examined in Chapter 2.
[b] I assumed that perennial crops, pasture, and hay were used at a ratio of 50% pasture : 50% hay.